DISTRIBUTION OF MARINE ZOOPLANKTON IN COASTAL WATERS OF SOUTHERN CHINA

TAM, PUI FUN

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Distribution of marine zooplankton in coastal waters of Southern China

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Tam, Pui Fun

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Department of Biology
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Abstract

This thesis consists of two parts. The first part studies the seasonal and spatial distribution of copepods in the Zhujiang River estuary. The second part examines diel changes in vertical and horizontal distribution and feeding activity of marine cladocerans in Tolo Harbour, Hong Kong.

The Zhujiang River is the largest river system in southern China. The Zhujiang River estuary is an important natural resource for the people of Guangdong and Hong Kong. The seasonal and spatial distribution of copepods were studied between June 1991 and October 1992 and between January 1995 and July 1996. During the study period, clear seasonal patterns in physical environmental parameters such as temperature, salinity, freshwater outflows and ocean currents were recorded. These environmental changes imposed great influences on copepod communities in the Zhujiang River estuary. A minimum of 49 copepod species were identified. Calanoida (at least 39 species) was the most dominant group in terms of numerical abundance and species diversity. The copepod community consisted of species of different origins. Some were endemic estuarine species adapted to brackish water. Some species were derived from coastal or oceanic waters, while others were of freshwater origin. Seven species, including *Acartia spinicauda*, *Acartiella sinensis*, *Calanus sinicus*, *Eucalanus subcrassus*, *Labidocera euchaeta*, *Paracalanus parvus* and *Pseudodiaptomus poplesia*, were considered dominant. Like many estuarine species, each dominant species occurred over wide ranges of temperatures and salinities. Seasonal succession and spatial segregation were exhibited by some of the dominant copepods.

Diel changes in distribution and feeding activity of marine cladocerans over small spatial scales along a transect from the inshore to offshore region in Tolo Harbour, a semi-enclosed inlet in Hong Kong, was studied on 23 May 1996. Four species of marine cladocerans, including *Pseudevadne tergestina*, *Penilia avirostris*, *Podon* sp. and *Pleopis schmackeri*, were found. Different species showed different patterns of spatial and temporal distribution. Within each species, the bigger and more conspicuous individuals tended to avoid the surface and inshore waters and stayed in the bottom and offshore areas during the day. Nocturnal upward migration by marine cladocerans in Tolo Harbour was probably not caused by the need to obtain more food from the surface water because food was abundant throughout the water column. The feeding activity of *P. tergestina* and *P. avirostris* was not related to diel vertical migration. Light increased the feeding activity of *P. tergestina* but decreased the feeding activity of *P. avirostris*. *P. tergestina*, *Podon* sp. and *P. schmackeri* have large compound eyes and strong raptorial appendages. Their surface- and inshore-dwelling behaviours suggested that they are raptorial feeders which feed during the day. *P. tergestina* and *P. avirostris* were observed to carry more conspicuous and mature embryos only at night. These observations suggested that the migratory, feeding and reproductive behaviours of marine cladocerans were adaptations to minimize risk to visual predators and increase feeding efficiency.

南中國近岸的海洋浮游生物分佈

摘要

本論文主要分爲兩個部份。第一部份論述浮游橈足類於珠江口內海區的季節性及空間分佈情況。第二部份則研討海洋枝角類於吐露港之晝夜垂直及平面分佈情況和攝食活動。

對於珠江口內海區的浮游橈足類的季節性和空間分佈情況於一九九一年六月至一九九二年十月及一九九五年一月至一九九六年七月間進行研究。從紀錄顯示，該段期間的環境因素如氣溫、鹽度、珠江徑流和海流都有明顯的季節性變化。這些環境因素的變化對於珠江口內海區的浮游橈足類群落的結構有重要的影響。在研究期內，發現了最少四十九種浮游橈足類。鏢水蚤目(Order Calanoida)無論在數量上或種類多樣化上都佔絕對優勢，共三十九個種類或以上。這些浮游橈足類的群落有不同的來源，其中包括適半鹹水的地方河口種類。有些則來自近岸、海洋甚或珠江口上游的淡水區域。刺尾紡錘鏢水蚤(*Acartia spinicauda*)、中華異水蚤(*Acartiella sinensis*)、中華哲水蚤(*Calanus sinicus*)、亞强壯眞哲鏢水蚤(*Eucalanus subcrassus*)、眞刺唇角鏢水蚤(*Labidocera euchaeta*)、小型擬哲鏢水蚤(*Paracalanus parvus*)和火腿僞鏢水蚤(*Pseudodiaptomus poplesia*)被定爲優勢種。正如大部份生活於河口的種類一樣，每一個優勢種都能適應廣泛的溫度和鹽度。其中一些優勢種展示了季節性更替和空間隔離的情況。

海洋枝角類的晝夜分佈和攝食活動變化研究於一九九六年五月二十三日在吐露遠岸至近岸的一條斷面進行。四個種類的海洋枝角類包括肥胖僧帽潘(*Pseudevadne tergestina*)、鳥喙尖頭潘(*Penilia avirostris*)、大眼潘屬(*Podon* sp.)和史氏大眼潘(*Pleopis schmackeri*)皆被發現。不同的種類顯現不同的空間和時間分佈模式。每個種類中體積較大和較顯而易見的個體於日間偏向停留在較深和遠岸的水域。因爲在吐露港設定的研究水域內的整個水體都能提供足夠的食物給其中的海洋枝角類，所以它們的夜間向上垂直移動的行爲應該並非爲了從表層攝取更多的食物。肥胖僧帽潘和鳥喙尖頭潘的攝食活動與晝夜垂直分佈並無關連。日光會增加肥胖僧帽潘的攝食活動，卻減少鳥喙尖頭潘的攝食活動。肥胖僧帽潘、大眼潘屬和史氏大眼潘均擁有大型的複眼及强而有力的捕食附肢。它們日間於表層與近岸居住的習性顯示它們是靠日光進行獵食活動的捕食者。據觀察所得，肥胖僧帽潘和鳥喙尖頭潘孕育的胚胎在夜間更成熟和更明顯。總體來說，海洋枝角類的晝夜移動、攝食活動及繁殖行爲該是爲了避免捕食者的捕獵和增加本身的攝食效率。

Chapter 1. General introduction

The objective of this thesis is to investigate the temporal and spatial distribution of selected groups of crustacean zooplankton in their particular marine habitats. This thesis consists of two parts. The first part focuses on the seasonal and spatial distribution of copepods in the Zhujiang River estuary. The study investigates the structure of the copepod community and tries to identify the controlling factors causing community changes. With rapid economic development in coastal cities around Guangdong in the last decade, growing population and pollution has posed great threat to the natural environment of the Zhujiang River estuary. The Zhujiang River estuary is an important natural resource for the people of Guangdong and Hong Kong. It is also a feeding and spawning ground for many commercially important fishes and shrimps. To develop effective environmental management programs to preserve this valuable resource, we need more baseline studies to understand the ecological dynamics of the estuarine system. Marine copepods are important components of the estuarine plankton. Information on taxonomic distribution and seasonal and spatial dynamics of copepods is still lacking.

The second part of the thesis examines diel changes in vertical and horizontal distribution and feeding activity of marine cladocerans over small spatial scales along a transect from the inshore to the offshore region in the middle of Tolo Harbour, a semi-enclosed embayment in Hong Kong. Previous studies of marine zooplankton in Tolo Harbour (Chan 1991; Wong *et al.* 1993) mainly focused on seasonal dynamics at a few widely spaced stations located along the harbour. Tang (1993) studied seasonal changes in the population of marine cladocerans in Tolo Harbour, but spatial distribution within the harbour was not mentioned. Studies of diel vertical migration

and feeding behaviour have so far been restricted to the several major copepod species in the harbour (Tang *et al.* 1994). Diel changes in vertical and horizontal distribution over small spatial scale as well as diel changes in feeding intensity have rarely been reported in marine cladocerans.

Chapter 2. Temporal and spatial distribution of Copepoda in the Zhujiang River estuary

2.1 Literature review

2.1.1 Physical properties of estuaries

An estuary is a semi-enclosed coastal body of water which has a free connection with the open sea and within which the seawater is measurably diluted with freshwater from land drainage (Ketchum 1983). Being boundaries zones between land and ocean where freshwater and seawater mix, estuaries vary remarkably in physical, chemical and biological properties that result in greater environmental stress and lower diversity of life than in other aquatic systems, even though the density of individual species may be great (Kennish 1986). Although every estuary exhibits a unique regime of physical conditions, they share common characteristics and no system is completely isolated from outside influences (Kennish 1986). Estuaries are characterized by their environmental gradients, both temporally and spatially (Soetart and Van-Rijswijk 1993). Annual periodicity in river discharge, salinity, temperature and surrounding ocean currents can be observed in estuaries.

Temperature follows the seasonal heating and cooling cycle, being highest in summer and lowest in winter. The seasonal pattern of river discharge produces a corresponding seasonal change in salinity in estuaries. Temporal variation in salinity is a principal feature of estuarine environments. During the rainy season, increase in river discharge dilutes the seawater and lowers the salinity in estuaries. During the dry season, high salinity prevails as the river discharge is reduced. Pronounced spatial

gradient in salinity is another important feature of estuaries. Salinity increases from the inner to the outer regions of estuaries. During periods of peak river discharge, a surface layer of lower salinity is produced (Edgar and Gresswell 1991). When water in the estuary has a strong density stratification in vertical direction because of strong freshwater discharge, a type of estuarine circulation with net seaward flow near the surface and net landward flow near the bottom is induced (Day *et al.* 1989). Origin of ocean currents that influence the outer regions of estuaries may vary with the monsoonal weather (Millar 1983; Chen 1992). For example, monsoonal change in Yaquina Bay (Oregon) drives an alternation of flow in the nearby ocean, with summer flow from the north and winter flow from the south (Millar 1983).

2.1.2 Factors affecting the zooplankton community

Ecologically, most estuaries are controlled by physical factors (Kennish 1986). Changes in temperature, river flow, salinity and coastal hydrography strongly affect the zooplankton community. Biological factors such as phytoplankton production and predation pressure probably play important, but secondary, roles in structuring the zooplankton community.

2.1.2.1 Temperature

Temporal changes in the zooplankton community can be induced by temperature (Ambler *et al.* 1985). The abundance of copepods is significantly correlated with water temperature in the North Carolina estuary (Mallin 1991). Temperature is an important factor that drives the seasonal succession of dominant

copepods in estuaries (Grice and Marcus 1981; Diouf and Dialls 1990; Palomares-Garcia and Gomez-Gutierrez 1996). For example, the seasonal succession of *Acartia clausi* (a cold-water form) by *Acartia tonsa* (a warm-water species) in the east coast of the United States during summer is probably controlled by temperature (Grice and Marcus 1981). The production and hatching of dormant eggs produced by copepods are also largely attributed to the seasonal change in temperature in estuaries (Grice and Marcus 1981; Millar 1983).

2.1.2.2 River discharge and salinity

Seasonal changes in river discharge are always accompanied by seasonal changes in salinity in estuaries (Millar 1983). In the estuarine system of the Mankyoung River and Dongjin River, large seasonal changes in salinity caused by monsoonal flooding are often associated with changes in the community structure of copepods (Suh *et al.* 1991). Day *et al.* (1989) also suggested that salinity may affect the overall composition of zooplankton in estuaries. Soetaert and Van-Rijswijk (1993) pointed out that intrusion of marine species begins in spring in the Westerschelde estuary. Marine species reach their most upstream distribution and highest densities in summer and early fall when river discharge is low and seawater protrudes deep into the estuary. Marine species decline and retreat from the estuary in winter when river discharge is high and the overall salinity in the estuary is low.

River flow can govern the movement of copepod populations along the estuary (Castel 1995). In Chesapeake Bay, large freshwater outflow during the spring flushes some freshwater zooplankton down the estuary and produces a seasonal maximum in abundance (Cronin *et al.* 1962).

2.1.2.3 Coastal hydrography

Changes in coastal hydrography may affect the seasonal occurrence of coastal copepods in estuaries (Jefferies 1962; Chen 1992). For example, northerly winds along the west coast of the United States produce upwelling during the spring and summer and bring fauna with northern zoogeographic affinities to the coastal areas (Jefferies 1962). During the winter, currents flowing north close to the coast bring along a different planktonic fauna with southern zoogeographic affinities. The seasonal occurrence of *Paracalanus parvus* was studied by Ambler *et al.* (1985). *P. parvus* is an oceanic indicator species which is absent in the estuarine system of San Francisco Bay between April and June when coastal currents are from the north of San Francisco Bay. *P. parvus* is found in the bay only during the winter when coastal waters are of southern origin .

2.1.2.4 Biological factors

Phytoplankton production and predation pressure are important biological factors that affect zooplankton abundance (Day *et al.* 1989; Fernex *et al.* 1996). Interactions between phytoplankton and zooplankton abundance cycles vary among estuaries and among years and seasons within the same estuary (Ambler *et al.* 1985). Day *et al.* (1989) suggested that estuarine zooplankton are much less dependent on phytoplankton than oceanic species because they can use suspended organic detritus and ciliates as food (Robertson 1983; Day *et al.* 1989). However, other studies have shown that phytoplankton production has great impacts on the abundance of

zooplankton. For example, Smayda (1983) observed that zooplankton biomass increases regularly after peaks in phytoplankton biomass in the Kiel Bight. Similarly, copepod decline in Villefranche Bay, an estuary in the northwest Mediterranean, has been related to the decrease in food levels after the phytoplankton decline (Fernex *et al.* 1996). Increase in the number of tentaculated ctenophores and jelly fishes is accompanied by decrease in the number of copepods in many estuarine systems (Day *et al.* 1989). Annual change in predation pressure may lead to change in the size of the copepod community (Hulsizer 1976). In Narragansett Bay, Hulsizer (1976) reported a sharp decline in the number of copepods in late summer and fall when the ctenophore *Mnemiopsis leidyi* is present.

2.1.3 Site description of the Zhujiang River estuary

The Zhujiang River estuary is located on the southern coast of China. The estuary receives a large amount of freshwater from the Zhujiang River, the largest river system in southern China, and is influenced by water masses from the South China Sea (Chau 1961; Morton and Morton 1983). The Zhujiang River consists of three large tributaries (Chen and Wei 1995), and has a watershed of 250,000 km^2. Turbid water flushing down into the estuary is enriched with sand, suspended particles and nutrients (Chau 1961; Morton and Morton 1983).

Seasonal variations in the physical environments of the Zhujiang River estuary are great. Average water temperature is the highest during summer (29.0°C) and becomes lower in autumn and winter (15.4°C) (Huang *et al.* 1995). The estuary is located in a typical monsoon climatic zone (Chen 1992). The dry northeast (NE) monsoon prevails in winter, while the wet southwest (SW) monsoon dominates during

summer. The monsoons alternate during spring and autumn when the direction of wind is changeable.

The origin of oceanic waters surrounding the Zhujiang River estuary changes seasonally. The southwestward drift current prevails in winter. The current is formed partly by the Kuroshio Current, which originates in the Pacific and enters the South China Sea through the Luzon Straits, and partly by the Taiwan Current, which originates in the East China Sea and enters the South China Sea through the Taiwan Strait (Morton and Morton 1983; Chen 1992). Some temperate planktonic species are carried into the South China Sea by currents flowing from NE to SW under the influence of the NE monsoon (Chen 1992). During the SW monsoon period in summer, northeastward drift current dominates the water mass surrounding the estuary (Chen 1992). Warm oceanic waters from the South China Sea flow from SW to NE and carry with it oceanic species from the northern parts of the South China Sea.

Salinity in the Zhujiang River estuary changes seasonally with the volume of river runoff. Salinity is high during winter when discharge from the Zhujiang River is weak (Fu *et al.* 1995). Oceanic water of high salinity flows into the inner parts of the estuary. Dilution starts in spring and continues through the summer. During periods of heavy rain in the summer, river runoff reaches a maximum and influence from the Zhujiang River is great. A strong vertical stratification is observed during the period of low salinity. A horizontal gradient with salinity increasing from the inner to the outer regions of the estuary is also observed in both dry and wet seasons (Huang *et al.* 1995). Because water flow from the Zhujiang River is diverged towards the west as a result of the earth's rotation (Chau 1961), the western part of estuary is more strongly influenced by freshwater and more diluted than the eastern part.

2.2 Introduction

Copepods are dominant components of the zooplankton in many estuaries (Millar 1983; Suh *et al.* 1991; Dias 1994; Gouda and Panigraphy 1995; Leitao *et al.* 1996). Copepods feed on phytoplankton and are fed upon by fish and the larvae of many commercially important marine invertebrates. Research on the temporal and spatial distribution of copepods in the Zhujiang River estuary is therefore of both practical and ecological importance.

Preliminary study on the taxonomy diversity of Copepoda in the Zhujiang River estuary was first conducted during 4 sampling cruises launched between June 1991 and March 1992 (Fu *et al.* 1995). A total of 28 copepod species were recorded. To provide more detailed information on the seasonal and spatial pattern of copepods in the estuary, eight sampling cruises were conducted after March 1992. Data from all 12 sampling cruises were combined and presented in this part of thesis.

The objectives of the present study are: 1) to study the seasonal and geographical patterns of copepod abundance and diversity in the Zhujiang River estuary, 2) to identify the temperature and salinity preference of the dominant copepod species; and 3) to investigate the seasonal succession and spatial segregation of copepods in the Zhujiang River estuary.

2.3 Materials and methods

A total of 12 cruises to the Zhujiang River estuary were launched between June 1991 and October 1992 and between January 1995 and July 1996. Twelve sampling stations were established, although not all 12 stations were visited in each cruise (Table 2.1). The location of 12 sampling stations is shown in Fig. 2.1.

At each sampling station, water samples were collected from surface and bottom for measurement of temperature, salinity and chlorophyll *a* concentration. Temperature was measured with a thermometer. Salinity was measured with a refractometer. Chlorophyll *a* concentration was measured spectrophotometrically (Parsons *et al.* 1984) by Mr. L. M. Huang of the South China Sea Institute of Oceanology.

Copepods were collected from each sampling station by making a single vertical haul from ~1 m above the bottom to the surface with a conical plankton net (0.5 m diameter and 667 μm mesh size). Zooplankton collected in the cod end was immediately preserved in 4% formaldehyde for enumeration in the laboratory. Copepods were identified to species levels whenever possible under a dissecting microscope according to Chen and Zhang (1965), Chen and Shen (1974), Chen *et al.* (1974) and Shen and Song (1979) with the help of Professor Q. C. Chen of the South China Sea Institute of Oceanology. At least 10% of each sample was counted and the abundance of each species was expressed in number of individuals per cubic meter (ind. m^{-3}).

Table 2.1 Sampling stations visited during each of the 12 cruises to the Zhujiang River estuary during 1991, 1992, 1995 and 1996.

Year	Day	Sampling stations
1991	22-23 Jun	S1, S3, S4, S5, S6, S8, S9, S10, S11, S12
	27-28 Sep	S1, S3, S4, S7, S9, S10, S11, S12
1992	19-20 Jan	S1, S3, S4, S7, S9, S10, S11, S12
	23-24 Mar	S1, S3, S4, S5, S8, S9, S10, S11
	7-8 Oct	S2, S4, S7, S9, S10
1995	15-16 Jan	S2, S4, S7, S10
	17-18 Apr	S2, S7, S8, S9, S10, S11
	12-13 Jul	S2, S4, S7, S9, S10, S11
	10-11 Oct	S2, S4, S7, S9, S10, S11
1996	17-18 Jan	S2, S4, S7, S9, S10, S11
	20-21 Apr	S1, S2, S3, S4, S5, S6, S7, S8, S9, S10, S11
	17-18 Jul	S2, S4, S6, S7, S9, S10, S11, S12

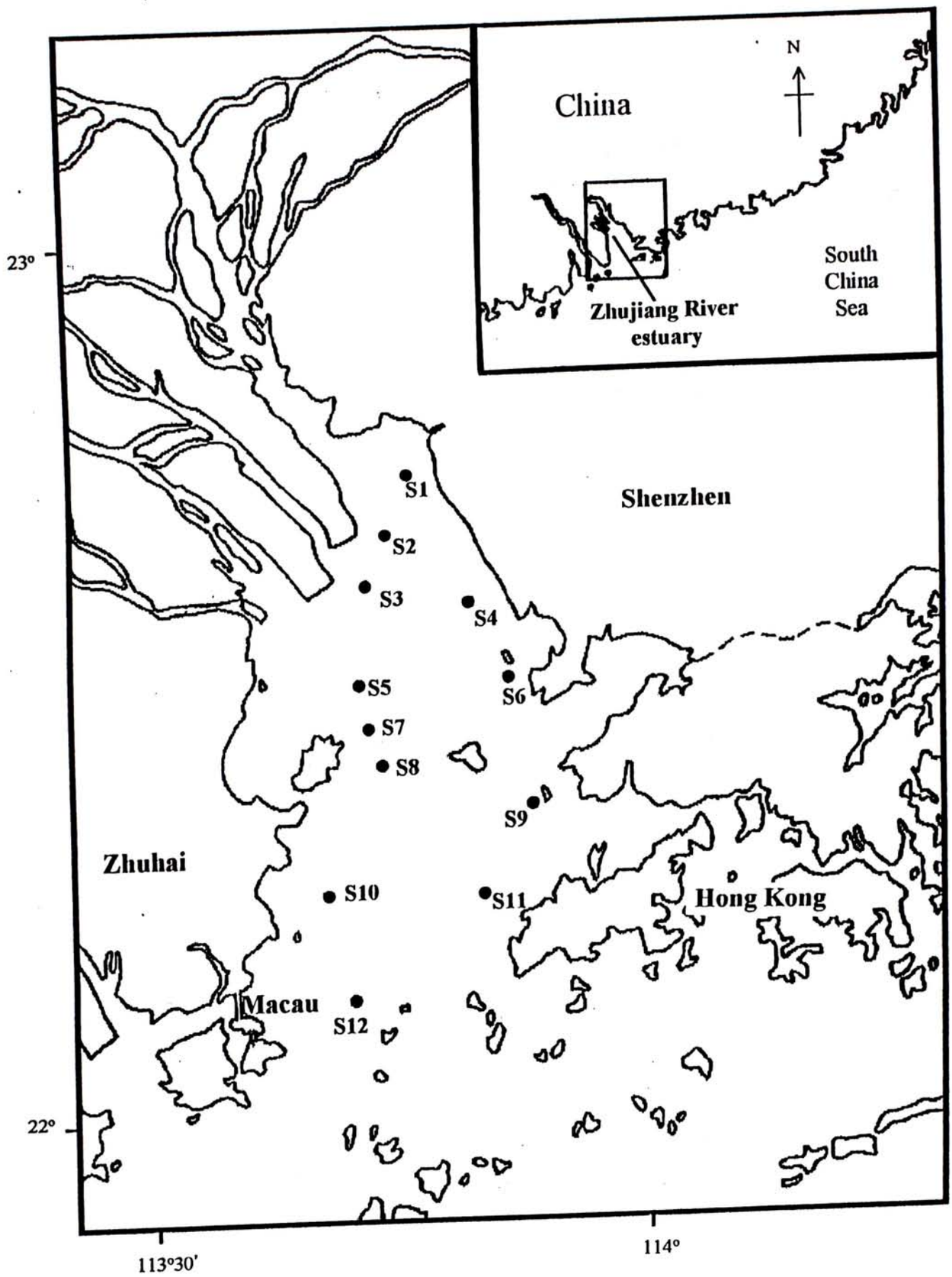


Fig.2.1 Map of the Zhujiang River estuary showing the location of 12 sampling stations

2.4 Results

2.4.1 Physical parameters and chlorophyll concentration

Fig. 2.2 presents the temporal and spatial variations in temperature and salinity in the Zhujiang River estuary. Water temperature was usually higher at the surface than in the bottom, although the difference was very slight. Strong seasonal pattern was observed. Water temperature was highest in summer and lowest in winter.

Salinity was usually lower in the surface than in the bottom. Values, recorded from 12 cruises, ranged from 0.7 to 31.0‰ in the surface and 1.0 to 34.7‰ in the bottom.

Marked spatial variations in salinity were observed in the Zhujiang River estuary. Salinity was lowest in the inner parts of the estuary near the mouth of river and increased progressively towards the outer parts of the estuary where oceanic influence was greater. The spatial difference in salinity was most pronounced during summer when river discharge from the Zhujiang River was at a peak and least obvious in winter when river discharge was negligible. Salinity was lower at S10 and S12 than at S9 and S11 because freshwater discharged from the river was diverted towards the western part of the estuary.

Salinity in the Zhujiang River estuary showed strong seasonal pattern. Salinity was high during the dry winter months when coastal water intruded deep into the estuary. No salinity stratification was observed. Salinity was only slightly lower in the surface than in the bottom. Salinity began to decrease in spring with the arrival of the wet southeast monsoon. Salinity stratification was observed during spring, summer and autumn.

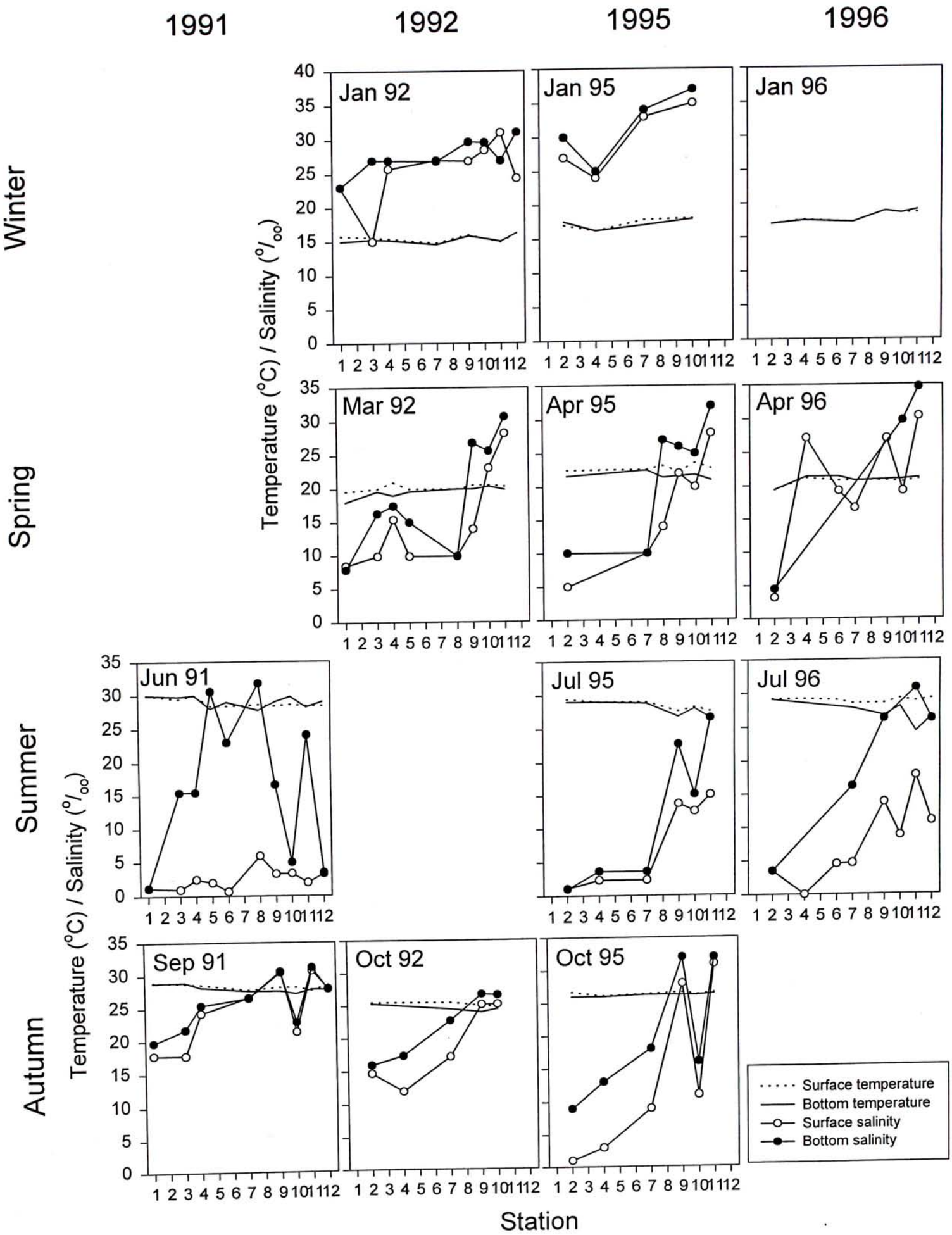


Fig. 2.2 Seasonal changes in temperature and salinity at 12 sampling stations in the Zhujiang River estuary.

No seasonal and spatial patterns in chlorophyll *a* concentration were observed (Fig. 2.3). Chlorophyll *a* concentration in the entire study area usually fluctuated below or around 5 ng mL^{-1}. Unusually high concentrations were recorded in September 1991 (autumn) and January 1992 (winter). Difference between the surface and bottom was not marked. Average concentration was higher in the surface than in the bottom in June 1991, January 1995, April 1995, July 1995 and July 1996. No clear vertical pattern in chlorophyll *a* concentration was observed during the other cruises.

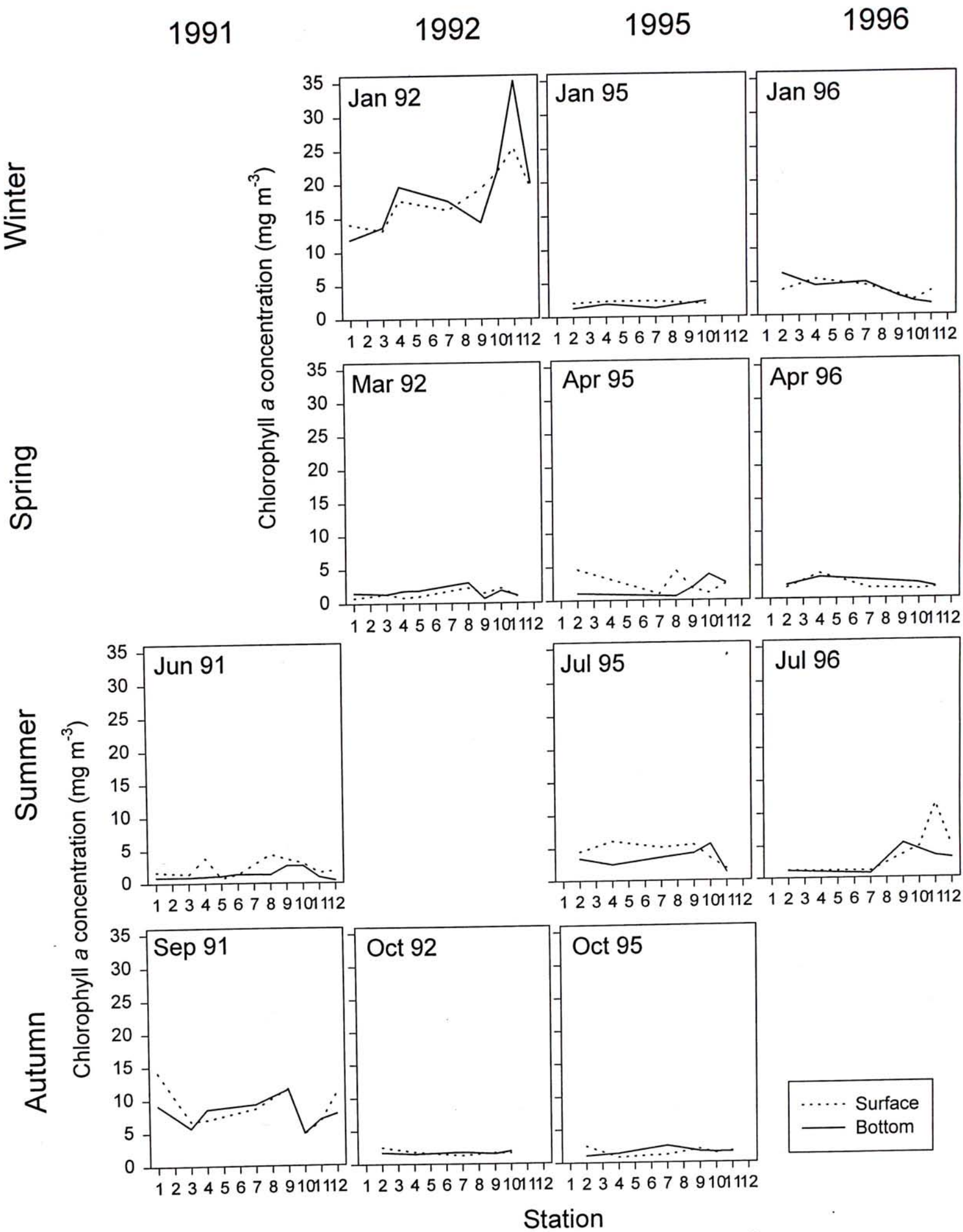


Fig. 2.3 Seasonal variations in chlorophyll *a* concentrations (mg m^{-3}) at 12 sampling stations in the Zhujiang River estuary.

2.4.2 Seasonal and spatial variations in the abundance of planktonic copepods

Seasonal patterns in the abundance of planktonic copepods in the Zhujiang River estuary during 1991, 1992, 1995 and 1996 are presented in Table 2.2. Copepoda was represented by a minimum of 49 species. Calanoida was the most important in terms of both species diversity (at least 39 species) and numerical abundance. Cyclopoida was represented by at least 9 species and Harpacticoida by only 1 species.

Among the 49 copepod species identified, 7 species were considered to be dominant in the estuary. Dominant species were arbitrarily defined as species that contributed > 25% of the total copepod abundance in at least one sampling cruise in this study. All 7 dominant copepods belonged to Order Calanoida. They included *Acartia spinicauda*, *Acartiella sinensis*, *Calanus sinicus*, *Eucalanus subcrassus*, *Labidocera euchaeta*, *Paracalanus parvus* and *Pseudodiaptomus poplesia*. No species of Cyclopoida and Harpacticoida was found to be dominant.

The remaining 42 species of less common copepods were divided into two groups: those occurring in more than one cruise (22 species) and those occurring in only one cruise (21 species). The total number of species from the two groups was assumed to be 42 because *Candacia* sp., which belonged to Group 1, and *Candacia simplex*, which belonged to Group 2, were counted as a single species when the two groups were combined. Species that occurred more than once were further divided into four subgroups according to their seasonal and spatial preferences. Subgroup 1 included species that showed clear seasonal and spatial patterns. Subgroup 2 consisted of species that showed clear seasonal patterns, but no spatial pattern. Subgroup 3 contained species with clear spatial pattern only, but no seasonal pattern. Subgroup 4 consisted of species that showed neither seasonal nor spatial patterns. Table 2.3 shows the spatial

Table 2.2 Mean seasonal densities (ind. m^{-3}) of planktonic copepods in the Zhujiang estuary during 1991, 1992, 1995 and 1996.

	1991		1992			1995				1996		
	Jun	Sep	Jan	Mar	Oct	Jan	Apr	Jul	Oct	Jan	Apr	Jul
Order Calanoida												
Family Acartiidae												
Acartia danae Giesbrecht, 1889	-	-	-	-	-	-	-	-	-	<1	-	-
Acartia erythrae Giesbrecht, 1889	-	-	-	-	-	-	-	-	<1		-	-
Acartia spinicauda Giesbrecht, 1889	32	17	32	18	22	53	23	43	30	161	76	39
Acartiella sinensis Shen & Lee, 1963	11	1	-	-	5	29	34	95	187	-	20	14
Family Calanidae												
Calanus sinicus Brodsky, 1962	<1	-	80	3	-	<1	8	<1	-	27	<1	1
Canthocalanus pauper (Giesbrecht, 1888)	-	1	-	-	7	-	-	-	29	<1	-	<1
Undinula darwinii (Lubbock, 1860)	-	-	-	-	-	-	-	-	1	-	-	-
Undinula vulgaris (Dana, 1849)	<1	<1	-	-	1	-	-	-	-	<1	-	-
Family Candaciidae												
Candacia simplex (Giesbrecht, 1889)	-	-	-	-	-	-	-	-	-	<1	-	-
Candacia sp.	-	<1	-	-	<1	-	-	-	-	-	-	-
Family Centropagidae												
Centropages furcatus (Dana, 1849)	-	<1	-	-	1	-	-	-	-	-	-	-
Centropages orsinii Giesbrecht, 1889	-	-	-	-	<1	-	-	-	-	-	-	-
Centropages tenuiremis Thompson & Scott, 1903	-	-	<1	<1	-	-	<1	-	-	<1	-	-
Sinocalanus sinensis (Poppe, 1895)	-	-	-	2	-	-	-	-	-	-	-	-
Family Diaptomidae												
Heliodiaptomus falxus Shen & Tai 1964	-	-	-	-	-	-	-	-	<1	-	-	-
Neodiaptomus schmackeri (Poppe & Richard, 1892)	-	-	-	-	-	-	-	-	-	-	-	<1
Phyllodiaptomus tunguidus Shen & Tai, 1964	-	-	-	-	-	-	-	-	<1	-	-	-
Family Eucalanidae												
Eucalanus subcrassus Giesbrecht, 1888	2	101	1	-	17	3	<1	<1	39	<1	-	2
Family Euchaetidae												
Euchaeta concinna Dana, 1849	-	1	<1	-	1	-	-	-	2	1	-	-
Euchaeta marina (Prestandrea, 1833)	-	<1	-	-	-	-	-	-	-	<1	-	-
Euchaeta sp.	-	-	-	-	-	<1	-	-	1	1	-	<1
Family Paracalanidae												
Acrocalanus gibber Giesbrecht, 1888	-	<1	-	-	4	-	-	-	1	-	-	-
Acrocalanus gracilis Giesbrecht, 1888	-	-	-	-	-	<1	-	-	-	<1	-	<1
Paracalanus aculeatus Giesbrecht, 1888	-	-	-	-	1	-	-	-	<1	1	-	-
Paracalanus crassirostris Dahl, 1893	1	1	-	-	1	-	-	1	1	33	-	<1
Paracalanus parvus (Claus, 1863)	-	-	1	<1	-	48	9	5	13	5	5	2

.....cont.

	1991		1992			1995				1996		
	Jun	Sep	Jan	Mar	Oct	Jan	Apr	Jul	Oct	Jan	Apr	Jul
Order Calanoida												
Family Pontellidae												
Calanopia thompsoni A. Scott, 1909	<1	5	-	-	-	-	-	-	7	-	1	-
Labidocera acuta (Dana, 1849)	-	<1	-	-	-	-	-	-	-	-	-	-
Labidocera bipinnata Tanaka, 1936	1	<1	-	<1	-	-	-	-	-	-	-	-
Labidocera euchaeta Giesbrecht, 1889	8	18	67	11	109	30	62	1	52	2	12	1
Labidocera pavo Giesbrecht, 1889	<1	<1	-	-	-	-	-	-	-	-	-	-
Pontellopsis regalis (Dana, 1849)	-	-	-	-	-	-	-	-	-	<1	-	-
Pontellopsis tenuicauda (Giesbrecht, 1889)	-	-	-	-	-	-	-	-	-	<1	-	-
Pontellopsis sp.	-	-	-	-	-	-	-	-	-	<1	-	-
Family Pseudocalanidae												
Clausocalanus furcatus (Brady, 1883)	-	-	-	-	-	-	-	-	-	<1	-	-
Family Pseudodiaptomidae												
Pseudodiaptomus poplesia (Shen, 1955)	6	-	-	85	-	2	480	7	-	-	80	3
Family Temoridae												
Temora discaudata Giesbrecht, 1889	-	<1	-	<1	-	-	1	<1	-	<1	<1	-
Temora gracilis Giesbrecht, 1889	-	-	<1	-	-	-	-	-	-	-	-	<1
Temora turbinata (Dana, 1849)	-	1	2	-	1	-	-	-	<1	<1	-	-
Family Tortanidae												
Tortanus dextrilobatus (Chen & Zhang 1965)	6	-	-	2	-	13	14	1	-	-	6	-
Tortanus forcipatus (Giesbrecht, 1889)	-	<1	-	-	<1	-	-	-	-	-	-	-
Tortanus gracilis (Brady, 1883)	1	-	<1	-	6	-	-	-	2	-	-	-
Order Cyclopoida												
Family Corycaeidae												
Corycaeus affinis McMurrich, 1916	-	-	<1	<1	1	-	2	-	<1	<1	3	-
Corycaeus catus F. Dahl, 1894	-	-	-	-	-	-	-	-	-	<1	-	-
Corycaeus crassiusculus Dana, 1849	-	-	-	-	-	-	-	-	-	<1	-	-
Corycaeus dahli Tanaka, 1957	-	-	-	-	-	-	-	-	<1	-	-	-
Corycaeus speciosus Dana, 1849	-	-	-	-	-	-	-	-	-	<1	-	-
Family Cyclopidae												
Halicyclops sp.	-	-	-	-	-	-	-	-	<1	-	-	-
Family Oithonidae												
Oithona decipiens Farran, 1913	-	-	-	-	-	-	-	-	<1	-	-	-
Oithona rigida Giesbrecht, 1896	-	-	-	1	-	-	-	<1	-	<1	-	<1
Oithona sp.	-	2	-	-	1	-	-	-	-	-	-	-
Family Oncaeidae												
Oncaea venusta Philippi, 1843	-	-	-	-	-	-	-	-	-	<1	-	-
Order Harpacticoida												
Family Ectinosomidae												
Microsettella norvegica (Boeck, 1846)	-	-	-	-	-	-	-	-	-	-	1	-

Table 2.3 Mean spatial densities (ind. m^{-3}) of planktonic copepods at 12 sampling stations in the Zhujiang estuary during 1991, 1992, 1995 and 1996

	Station											
	S1	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**	**S9**	**S10**	**S11**	**S12**
Order Calanoida												
Family Acartiidae												
Acartia danae Giesbrecht, 1889	-	-	-	-	-	-	-	-	-	-	<1	-
Acartia erythrae Giesbrecht, 1889	-	-	-	-	-	-	-	-	<1	-	<1	-
Acartia spinicauda Giesbrecht, 1889	56	70	24	66	18	50	38	33	43	54	33	9
Acartiella sinensis Shen & Lee, 1963	11	84	23	54	5	29	70	2	8	10	1	4
Family Calanidae												
Calanus sinicus Brodsky, 1962	10	-	14	2	-	-	10	1	21	8	15	39
Canthocalanus pauper (Giesbrecht, 1888)	-	1	-	-	-	-	10	-	2	1	4	<1
Undinula darwinii (Lubbock, 1860)	-	-	-	-	-	-	1	-	-	-	-	-
Undinula vulgaris (Dana, 1849)	-	-	-	-	-	-	<1	1	-	<1	<1	<1
Family Candaciidae												
Candacia simplex (Giesbrecht, 1889)	-	-	-	-	-	-	-	-	-	-	<1	-
Candacia sp.	-	-	-	-	-	-	<1	-	-	-	-	<1
Family Centropagidae												
Centropages furcatus (Dana, 1849)	-	-	-	-	-	-	<1	-	<1	-	<1	-
Centropages orsinii Giesbrecht, 1889	-	-	-	-	-	-	-	-	<1	-	-	-
Centropages tenuiremis Thompson & Scott, 1903	-	-	<1	<1	-	-	-	-	<1	<1	<1	-
Sinocalanus sinensis (Poppe, 1895)	3	-	-	-	-	-	-	-	-	-	-	-
Family Diaptomidae												
Heliodiaptomus falxus Shen & Tai 1964	-	-	-	<1	-	-	-	-	-	-	-	-
Neodiaptomus schmackeri (Poppe & Richard, 1892)	-	<1	-	-	-	-	-	-	-	-	-	-
Phyllodiaptomus tunguidus Shen & Tai, 1964	-	-	-	<1	-	-	-	-	-	-	-	-
Family Eucalanidae												
Eucalanus subcrassus Giesbrecht, 1888	-	4	1	6	-	<1	34	1	19	6	12	76
Family Euchaetidae												
Euchaeta concinna Dana, 1849	-	-	-	-	-	-	<1	-	<1	-	1	<1
Euchaeta marina (Prestandrea, 1833)	-	-	-	-	-	-	-	-	-	<1	-	1
Euchaeta sp.	-	-	-	-	-	-	-	-	<1	1	<1	-
Family Paracalanidae												
Acrocalanus gibber Giesbrecht, 1888	-	-	1	-	-	-	-	-	1	<1	2	<1
Acrocalanus gracilis Giesbrecht, 1888	-	<1	-	-	-	-	-	-	-	<1	<1	-
Paracalanus aculeatus Giesbrecht, 1888	-	-	-	-	-	-	-	-	<1	-	1	-
Paracalanus crassirostris Dahl, 1893	1	11	1	11	-	-	1	-	1	<1	1	-
Paracalanus parvus (Claus, 1863)	-	3	-	2	<1	2	20	9	4	12	4	-

.....continue

	Station											
	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12
Order Calanoida												
Family Pontellidae												
Calanopia thompsoni A. Scott, 1909	<1	-	3	1	-	<1	4	1	<1	2	<1	<1
Labidocera acuta (Dana, 1849)	-	-	-	-	-	-	-	-	-	-	-	<1
Labidocera bipinnata Tanaka, 1936	<1	-	-	-	-	-	-	-	-	-	2	<1
Labidocera euchaeta Giesbrecht, 1889	103	102	27	10	8	12	42	34	2	7	7	15
Labidocera pavo Giesbrecht, 1889	<1	-	<1	-	-	-	-	<1	-	-	-	-
Pontellopsis regalis (Dana, 1849)	-	-	-	-	-	-	-	-	-	-	<1	-
Pontellopsis tenuicauda (Giesbrecht, 1889)	-	-	-	-	-	-	-	-	-	<1	-	-
Pontellopsis sp.	-	-	-	-	-	-	-	-	-	-	<1	-
Family Pseudocalanidae												
Clausocalanus furcatus (Brady, 1883)	-	-	-	-	-	-	-	-	<1	<1	-	-
Family Pseudodiaptomidae												
Pseudodiaptomus poplesia (Shen, 1955)	175	122	125	5	<1	8	204	-	1	-	-	-
Family Temoridae												
Temora discaudata Giesbrecht, 1889	-	-	-	-	-	-	-	<1	<1	-	<1	<1
Temora gracilis Giesbrecht, 1889	-	-	-	-	-	-	-	-	<1	-	-	-
Temora turbinata (Dana, 1849)	-	-	<1	-	-	-	1	-	1	<1	<1	1
Family Tortanidae												
Tortanus dextrilobatus (Chen & Zhang 1965)	3	1	15	4	-	2	8	<1	<1	<1	2	-
Tortanus forcipatus (Giesbrecht, 1889)	-	-	<1	-	-	-	-	-	1	-	-	-
Tortanus gracilis (Brady, 1883)	-	<1	<1	-	-	-	-	-	<1	-	4	<1
Order Cyclopoida												
Family Corycaeidae												
Corycaeus affinis McMurrich, 1916	<1	<1	-	1	-	3	<1	1	<1	1	1	-
Corycaeus catus F. Dahl, 1894	-	-	-	-	-	-	-	-	<1	-	-	-
Corycaeus crassiusculus Dana, 1849	-	-	-	-	-	-	-	-	-	-	<1	-
Corycaeus dahli Tanaka, 1957	-	-	-	-	-	-	-	-	-	-	<1	-
Corycaeus speciosus Dana, 1849	-	-	-	-	-	-	-	-	-	<1	-	-
Family Cyclopidae												
Halicyclops sp.	-	<1	-	-	-	-	-	-	-	-	-	-
Family Oithonidae												
Oithona decipiens Farran, 1913	-	-	-	-	-	-	-	-	-	-	<1	-
Oithona rigida Giesbrecht, 1896	1	-	-	<1	-	-	-	-	<1	<1	-	-
Oithona sp.	4	-	-	<1	-	-	-	-	-	-	<1	-
Family Oncaeidae												
Oncaea venusta Philippi, 1843	-	-	-	-	-	-	-	-	-	-	<1	-
Order Harpacticoida												
Family Ectinosomidae												
Microsettella norvegica (Boeck, 1846)	-	-	-	-	-	-	-	-	-	1	-	-

distribution of planktonic copepods in the Zhujiang River estuary. *Acrocalanus gibber*, *Canthocalanus pauper*, *Euchaeta concinna* and *Temora turbinata* belonged to Subgroup 1. *A. gibber* and *C. pauper* occurred in the outer estuary during the autumn. *E. concinna* and *T. turbinata* were found in the outer estuary during autumn and winter. *Centropages tenuiremis* and *Tortanus forcipatus* belonged to Subgroup 2. Both species occurred throughout the estuary. *C. tenuiremis* occurred during winter and spring whle *T. forcipatus* was found only during autumn. Subgroup 3 included at least 8 species. *Candacia* sp., *Centropages furcatus*, *Paracalanus aculeatus*, *Euchaeta marina*, *Euchaeta* sp., *Temora discaudata*, *Temora gracilis* and *Undinula vulgaris* occurred in the outer estuary, while the *Paracalanus crassirostris* was found mainly in the inner estuary. Only 8 species were claimed in Subgroup 3 because *E. marina* and *Euchaeta* sp. were counted conservatively as a single species. All 8 species occurred sporadically throughout the year and showed no seasonal pattern of occurrence. *Acrocalanus gracilis*, *Calanopia thompsoni*, *Labidocera bipinnata*, *Labidocera pavo*, *Tortanus dextrilobatus*, *Tortanus gracilis*, *Corycaeus affinis*, *Oithona rigida* and *Oithona* sp. belonged to Subgroup 4. These species occurred in both the inner and outer parts of the estuary and showed no seasonal pattern of occurrence.

Among the 21 species which occurred only once during the study period, at least 14 species occurred only in the outer estuary during autumn and winter when water temperature was lower and the estuary was dominated by water masses from the South China Sea. *Acartia danae*, *Candacia simplex*, *Clausocalanus furcatus*, *Pontellopsis regalis*, *Pontellopsis tenuicauda*, *Pontellopsis* sp., *Corycaeus catus*, *Corycaeus crassiusculus*, *Corycaeus speciosus*, *Oncaea venusta* were found only during the winter. On the other hand, *Acartia erythrae*, *Centropages orsinii*, *Labidocera acuta*, *Corycaeus dahli*, *Oithona decipiens* were found only in autumn. All 14 species (as *Pontellopsis*

tenuicauda and *Pontellopsis* sp. were counted as a single species) were restricted to waters to the south of S9 where salinity >25‰.

Four freshwater calanoid copepods: *Heliodiaptomus falxus*, *Neodiaptomus schmackeri*, *Phyllodiaptomus tunguidus* and *Sinocalanus sinensis* were found in the samples. The 4 species were restricted to the inner estuary where salinity was <13‰ and were never found during winter when salinity was high throughout the entire estuary.

No conclusion can be drawn about the seasonal and spatial occurrence of *Halicyclops* sp., *Microsettella norvegica* and *Undinula darwinii*.

Seasonal variations in copepod abundance were great (Fig. 2.4). Densities ranged from 63 ind. m^{-3} in July 1996 to 632 ind. m^{-3} in April 1995. No clear seasonal patterns were observed, although densities were usually lower during period of maximum river discharge in the summer (June and July).

The density of copepods was usually below 250 ind. m^{-3}. Peaks in copepod density were observed in April and October 1995. The peak in April 1995 was mainly due to the occurrence of dense populations of *Pseudodiaptomus poplesia* in the inner parts of the estuary.

Table 2.4 presents the seasonal variations in species diversity among Calanoida, Cyclopoida and Harpacticoida. The total number of species was usually higher during autumn and winter. The highest total number of species recorded (26 species) was recorded during January 1996. Species diversity was higher towards the outer regions of the estuary (Table 2.5). The lowest total number of species (5 species) was recorded in S5 and the highest was found in S11 (30 species).

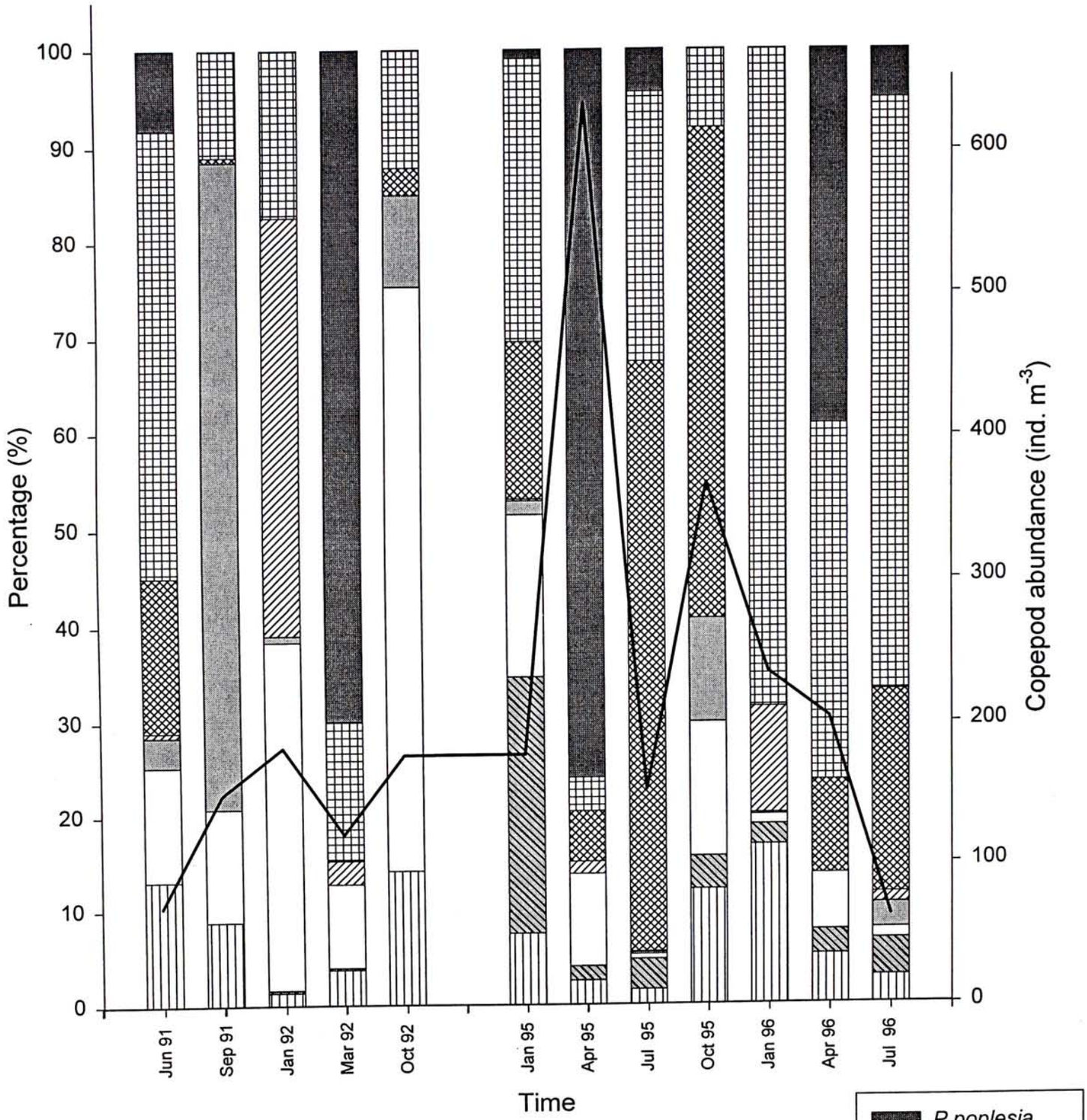


Fig. 2.4 Seasonal variations in copepod abundance (solid line) in the Zhujiang River estuary during 1991, 1992, 1995 and 1996. Vertical bars represent the relative abundance of dominant species of copepods.

Table 2.4 Summary of seasonal variations in species diversity of planktonic copepods in the Zhujiang River estuary.

	1991		1992			1995				1996		
Order	**Jun**	**Sep**	**Jan**	**Mar**	**Oct**	**Jan**	**Apr**	**Jul**	**Oct**	**Jan**	**Apr**	**Jul**
Calanoida	13	19	10	10	16	10	10	10	17	20	9	13
Cyclopoida	-	1	1	2	2	-	1	1	4	6	1	1
Harpacticoida	-	-	-	-	-	-	-	-	-	-	1	-
Total no. of species	13	20	11	12	18	10	11	11	21	26	11	14

Table 2.5 Summary of spatial variations in species diversity of planktonic copepods in the Zhujiang River estuary.

	Station											
Order	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**	**S9**	**S10**	**S11**	**S12**
Calanoida	10	12	15	13	5	8	17	11	24	18	25	17
Cyclopoida	3	2	-	2	-	1	1	1	3	3	5	-
Harpacticoida	-	-	-	-	-	-	-	-	-	1	-	-
Total no. of species	13	14	15	15	5	9	18	12	27	22	30	17

2.4.3 Seasonal variations in the relative abundance of the 7 dominant copepods.

Fig. 2.4 presents the seasonal variations in the relative abundance of 7 dominant copepods in the Zhujiang River estuary. The 7 dominant species were *Acartia spinicauda*, *Acartiella sinensis*, *Calanus sinicus*, *Eucalanus subcrassus*, *Labidocera euchaeta*, *Paracalanus parvus* and *Pseudodiaptomus poplesia*. The 7 species always contributed >80% of the total copepod abundance.

Acartia spinicauda and *Labidocera euchaeta* were found in every sampling cruise and were the only perennial copepods in the estuary. Relative abundance >60% was recorded for *A. spinicauda* in January 1996 and July 1996 and for *L. euchaeta* in October 1992. *Acartiella sinensis* constituted >50% of the copepod community in July 1995 and October 1995. *Calanus sinicus*, which was usually rare, reached a peak in January 1992 and accounted for 43.5% of copepod community. *Eucalanus subcrassus* formed 68% of the copepod community in September 1991, but was uncommon or even absent in some of the sampling cruises. *Paracalanus parvus* usually appeared as a minor component (<4%) of the copepod community, but reached a peak in January 1995 and formed 27.2% of the copepod community. *Pseudodiaptomus poplesia* tended to become dominant during the spring (March 1992, April 1995 and April 1996). Its contribution to copepod community was ~70% in March 1992 and April 1995 and ~40% in April 1996.

2.4.4 Relationship between copepod abundance and chlorophyll *a* concentration

Fig. 2.5 presents the relationship between the total copepod abundance and mean chlorophyll *a* concentration in the Zhujiang River estuary. Visual inspection of The data revealed that copepod abundance was highly variable at chlorophyll *a* concentration <5 mg m^{-3} and consistently low at chlorophyll *a* concentration >10 mg m^{-3}. Correlation between copepod abundance and chlorophyll *a* concentration was tested using simple linear (R^2=0.0131, P>0.05), logarithm (R^2=0.0029, P>0.05) and exponential (R^2=0.0027, P>0.05) models. No significant correlation was found, suggesting that there was no relationship between the magnitude of the two variables. Similarly, no correlation was found between the abundance of each of the 7 dominant copepods and the mean chlorophyll *a* concentration.

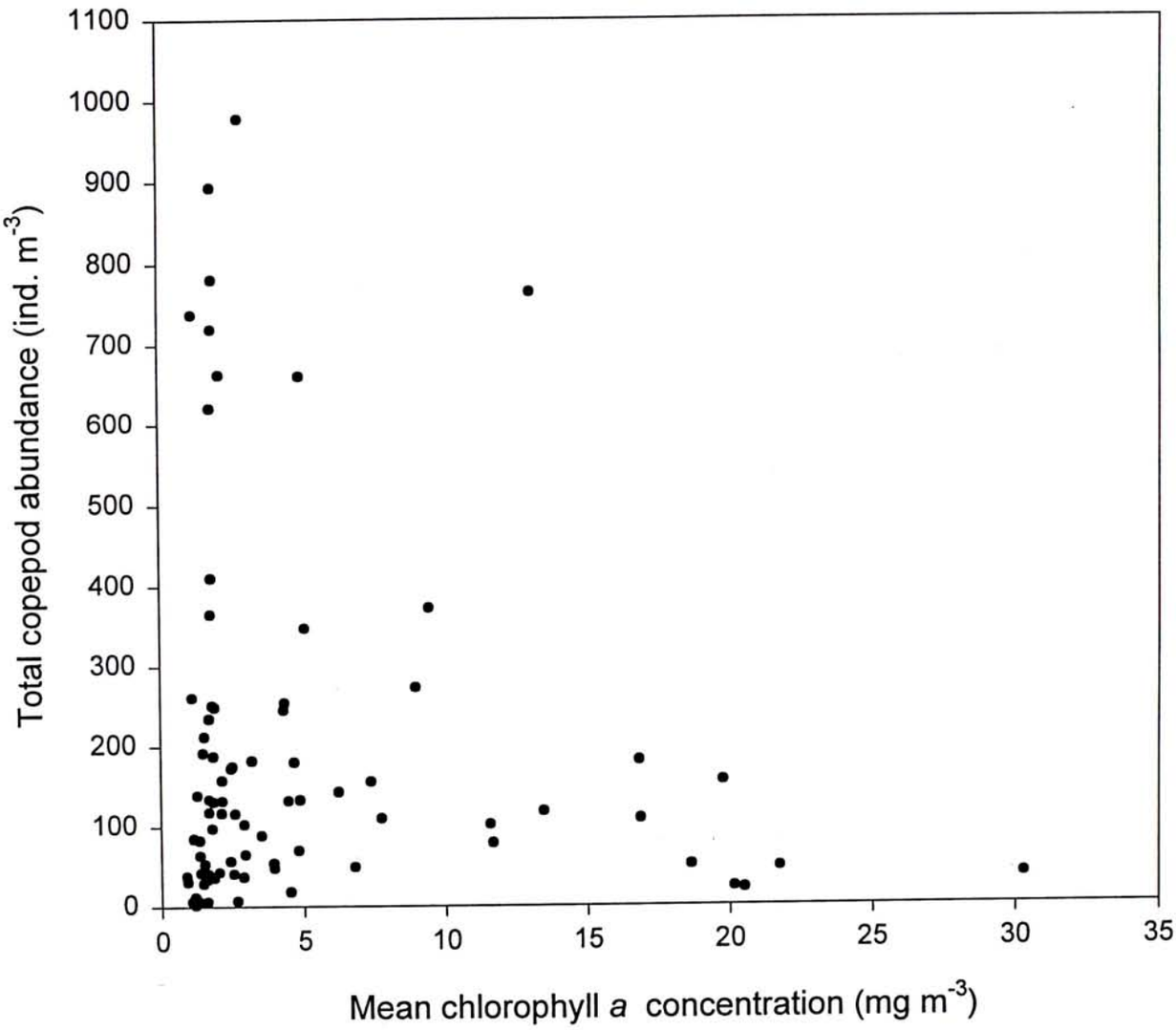


Fig. 2.5 Relationship between total copepod abundance and mean chlorophyll *a* concentration in the Zhujiang River estuary during 1991, 1992, 1995 and 1996. Each dot represents the total copepod abundance at the respective ambient chlorophyll *a* concentration in each station.

2.4.5 Seasonal and spatial distribution and salinity and temperature preference of dominant copepods

The seasonal and spatial distribution patterns of the 7 dominant copepods in the Zhujiang River estuary are presented in Fig. 2.6 to Fig. 2.12. The species-specific preference in temperature and salinity for all 7 dominant copepods is presented in Fig. 2.13. Estuarine zooplankton tend to have broad physiological tolerances to ensure survival in the highly variable conditions of estuaries (Day *et al.* 1989). Similarly, copepods which were found to be dominant in the Zhujiang River estuary tended to tolerate a wide range of salinity and temperature.

Acartia spinicauda was one of the two copepods that occurred throughout the year in the Zhujiang River estuary (Fig. 2.6). The highest densities were recorded in January 1996. Seasonal change in spatial distribution was observed in the population. Dense populations were mostly found in the inner regions of the estuary during January when freshwater runoff from the Zhujiang River was low. A shift of the main population to the outer estuary occurred during the mid-spring (April) and early summer (June and July) when river discharge increased. Distribution in the estuary became more even in autumn (September and October) when *A. spincauda* began to appear again in the inner regions of the estuary. *A. spinicauda* was widely distributed in temperatures ranging from 15.3 to 29.2°C and salinities from 3.8 to 36.0‰ (Fig. 2.13). Dense populations occurred mainly in salinities ranging from 10 to 24.5‰.

The seasonal occurrence of *Acartiella sinensis* in the Zhujiang River estuary was sporadic (Fig. 2.7). Although a density of 490 ind. m^{-3} was recorded in January 1992, the species was absent in January 1996. Similarly, while only low numbers were found in September 1991 and October 1992, much higher densities were recorded in the inner

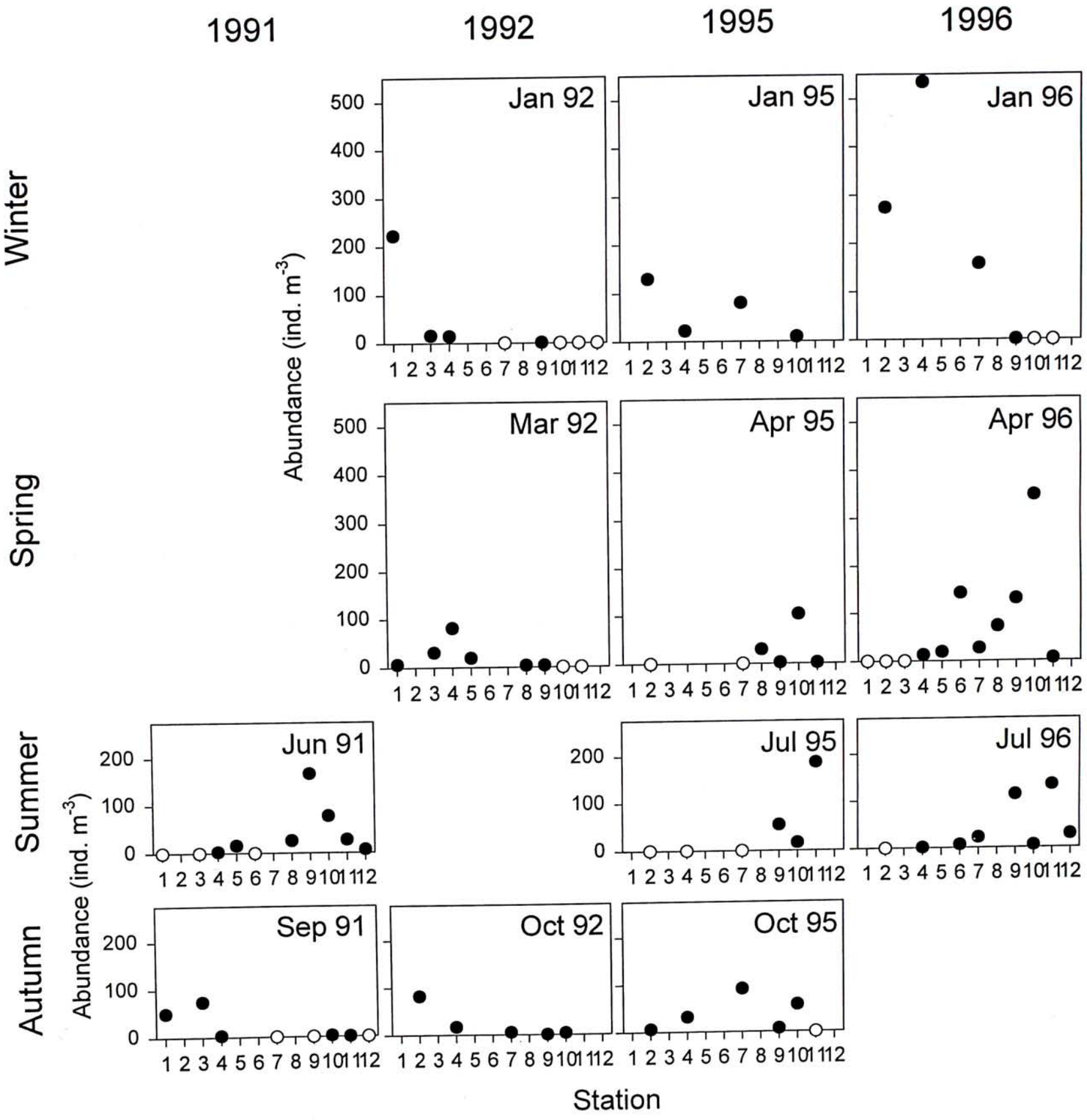


Fig. 2.6 Seasonal and spatial distribution of *Acartia spinicauda* in 12 sampling stations in the Zhujiang River estuary during 1991, 1992, 1995 and 1996. Solid circles represent the presence of *A. spinicauda*. Open circles represent the absence of *A. spinicauda*.

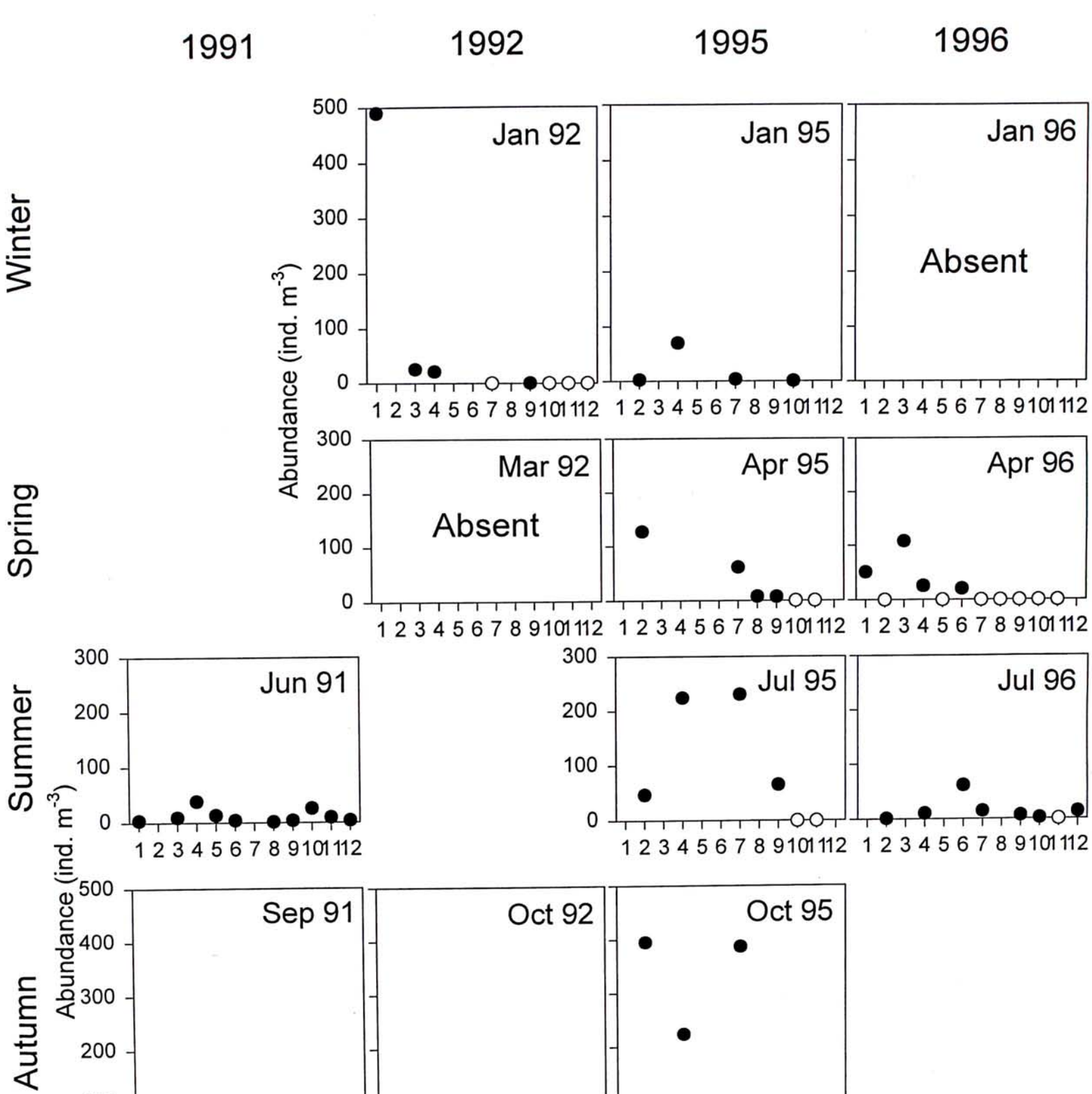


Fig. 2.7 Seasonal and spatial distribution of *Acartiella sinensis* in 12 sampling stations in the Zhujiang River estuary during 1991, 1992, 1995 and 1996. Solid circles represent the presence of *A. sinensis*. Open circles represent the absence of *A. sinensis*.

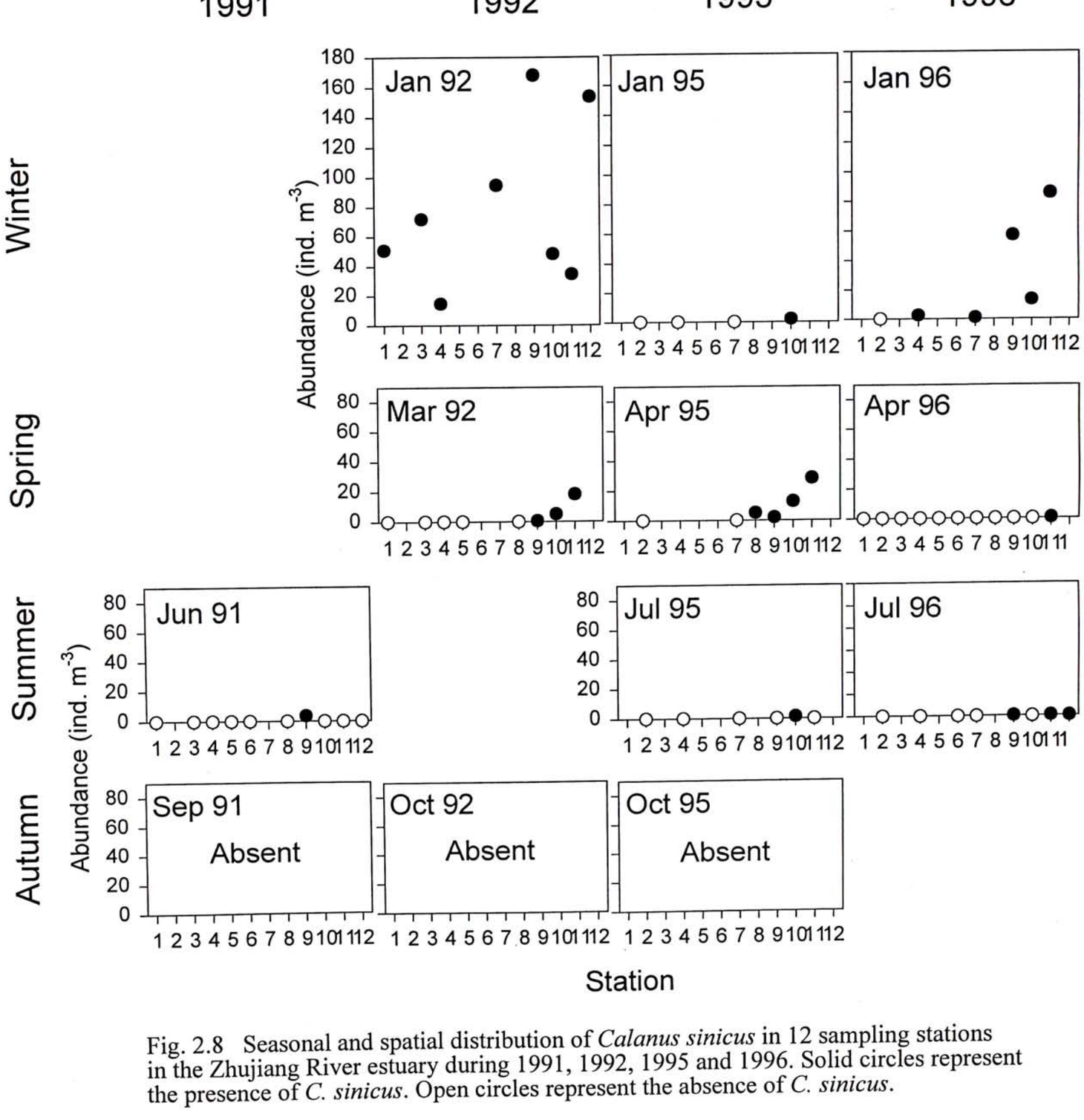


Fig. 2.8 Seasonal and spatial distribution of *Calanus sinicus* in 12 sampling stations in the Zhujiang River estuary during 1991, 1992, 1995 and 1996. Solid circles represent the presence of *C. sinicus*. Open circles represent the absence of *C. sinicus*.

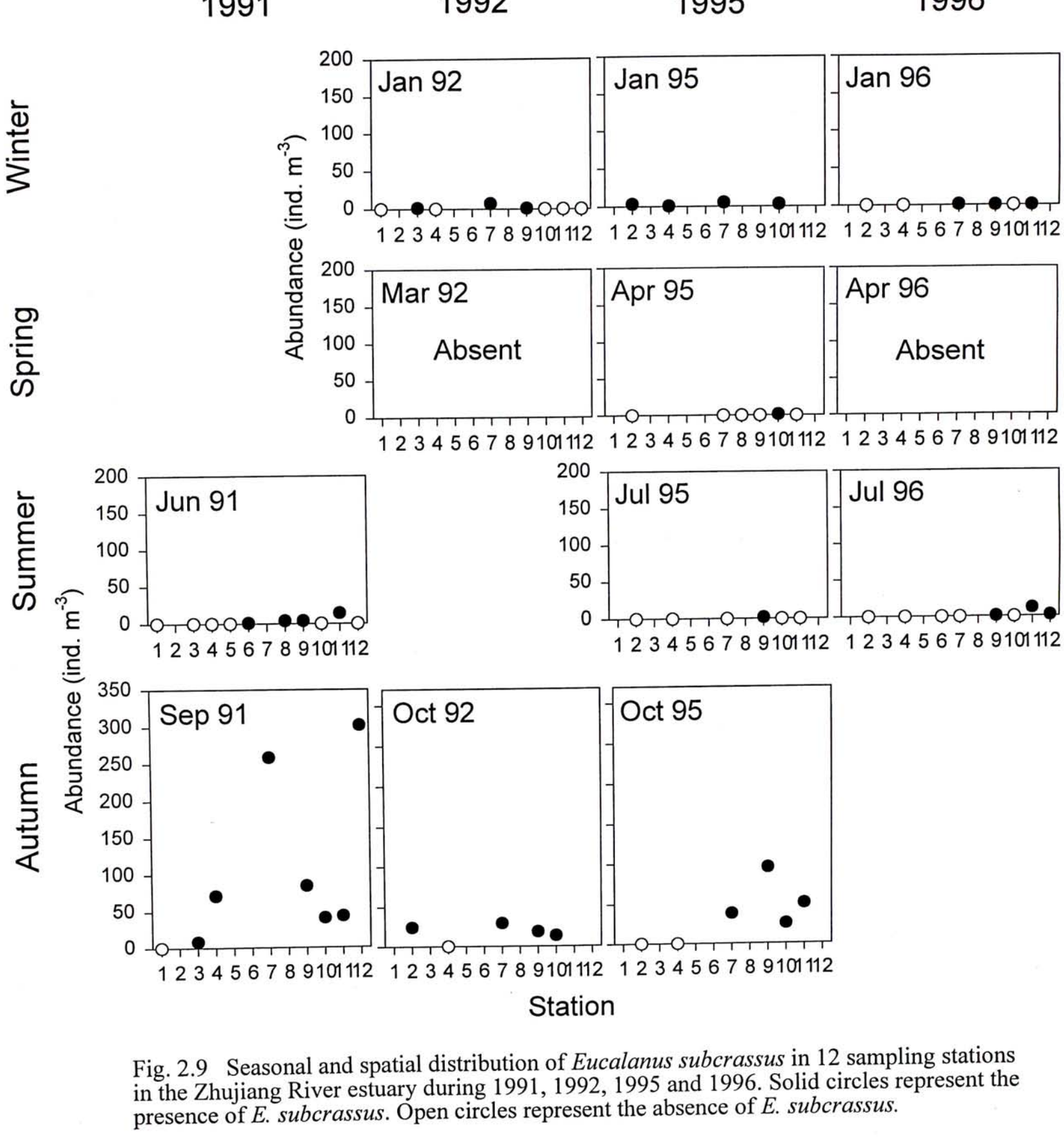


Fig. 2.9 Seasonal and spatial distribution of *Eucalanus subcrassus* in 12 sampling stations in the Zhujiang River estuary during 1991, 1992, 1995 and 1996. Solid circles represent the presence of *E. subcrassus*. Open circles represent the absence of *E. subcrassus*.

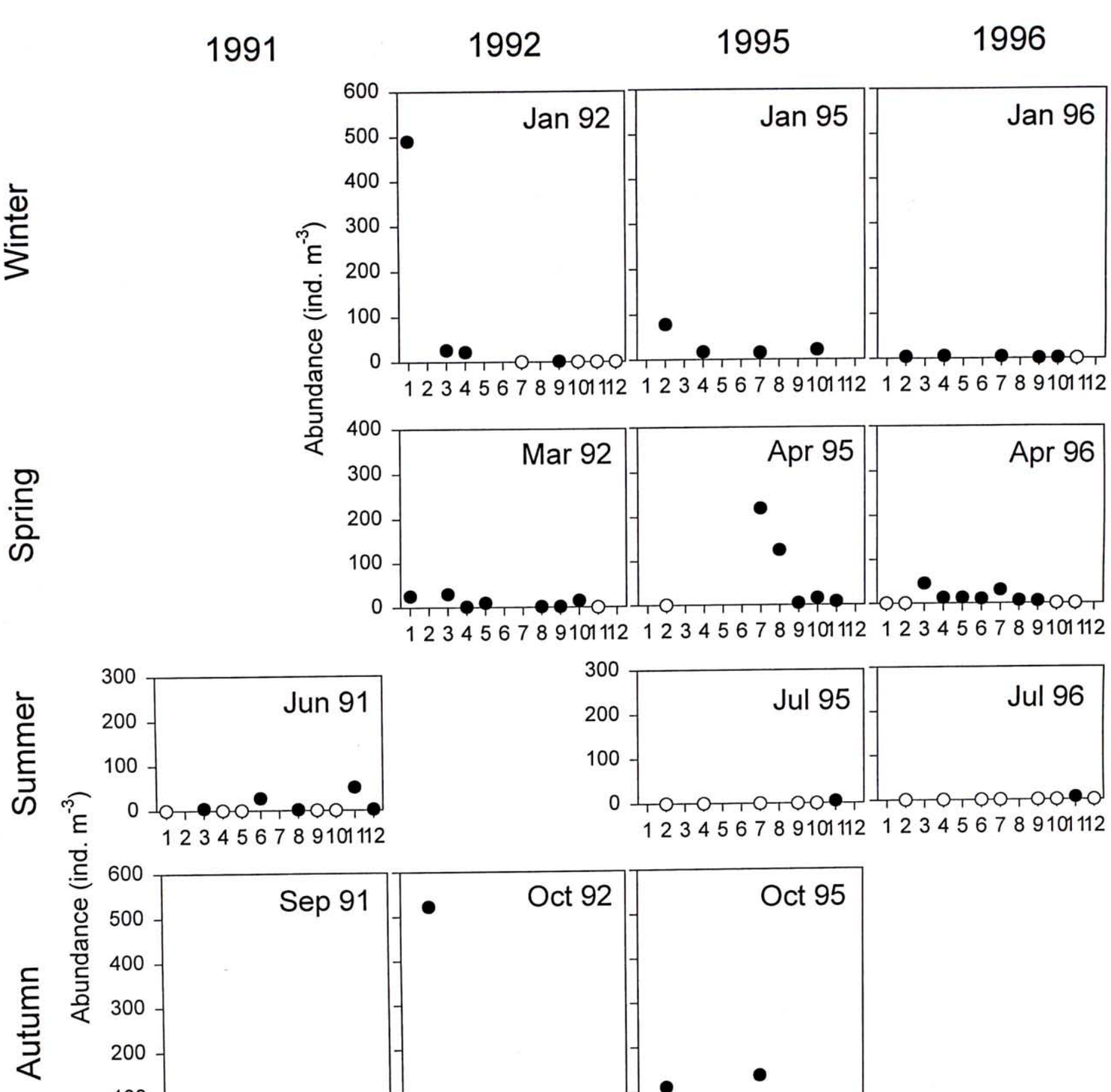


Fig. 2.10 Seasonal and spatial distribution of *Labidocera euchaeta* in 12 sampling stations in the Zhujiang River estuary during 1991, 1992, 1995 and 1996. Solid circles represent the presence of *L. euchaeta*. Open circles represent the absence of *L. euchaeta*.

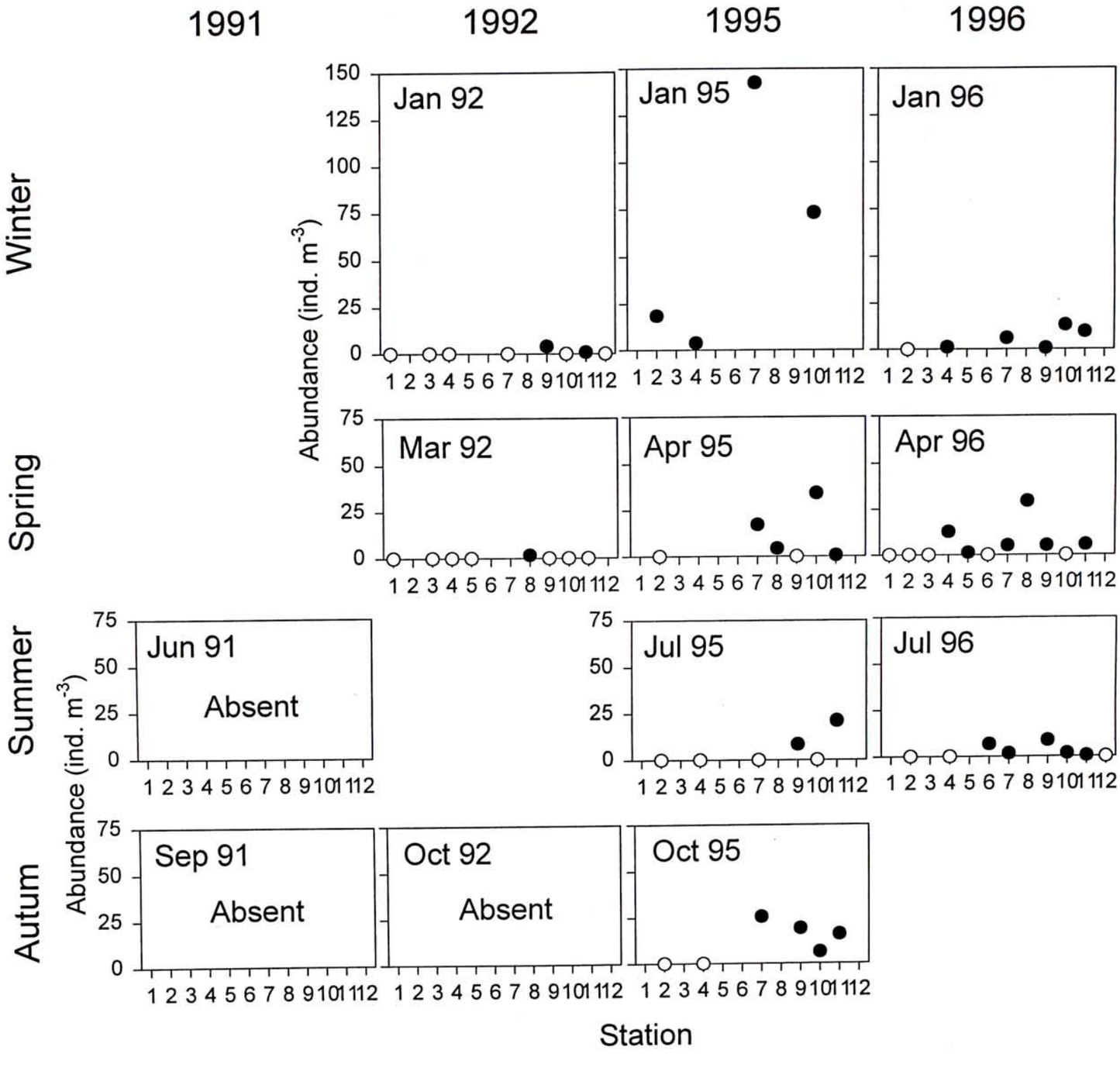


Fig. 2.11 Seasonal and spatial distribution of *Paracalanus parvus* in 12 sampling stations in the Zhujiang River estuary during 1991, 1992, 1995 and 1996. Solid circles represent the presence of *P. parvus.* Open circles represent the absence of *P. parvus*.

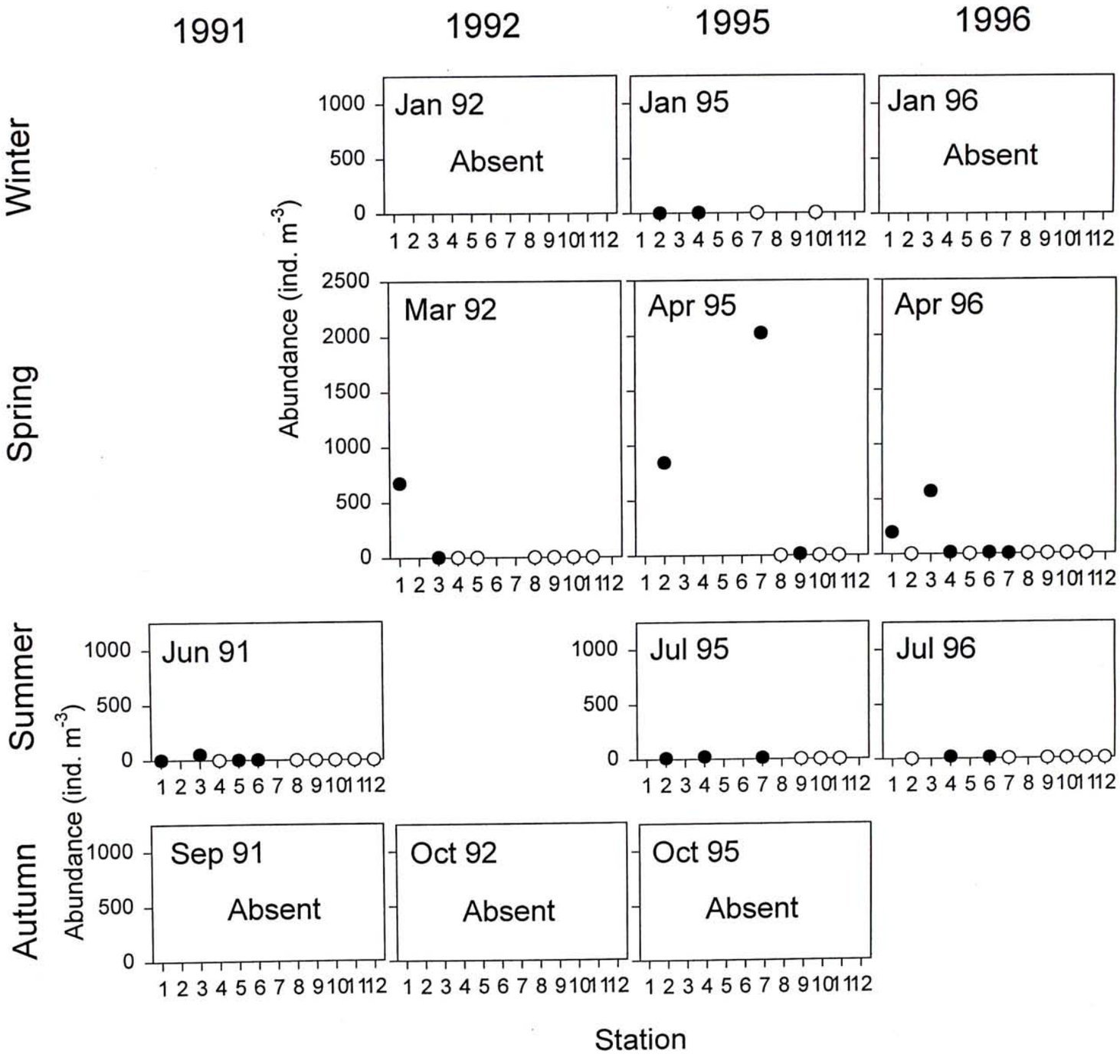


Fig. 2.12 Seasonal and spatial distribution of *Pseudodiaptomus poplesia* in 12 sampling stations in the Zhujiang River estuary during 1991, 1992, 1995 and 1996. Solid circles represent the presence of *P. poplesia*. Open circles represent the absence of *P. poplesia*.

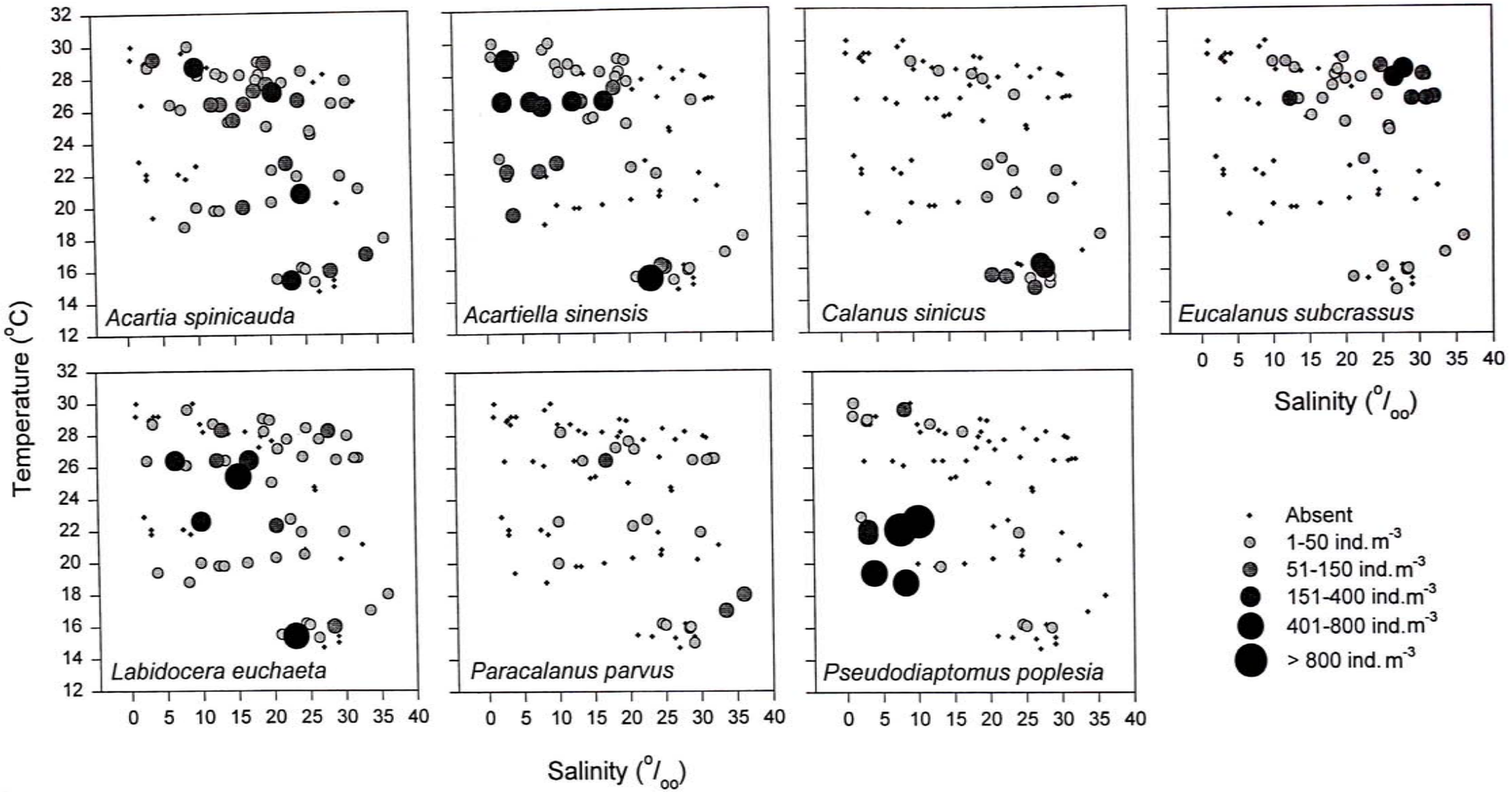


Fig. 2.13 Range of temperature and salinity for the occurrence of the 7 dominant copepods in the Zhujiang River estuary.

parts of the estuary during October 1995. *A. sinensis* preferred to stay in the inner estuary where salinity was low during most of the year. Fig. 2.13 shows that *A. sinensis* occurred in a wide range of temperatures from 15.4 to 28.9°C. The species appeared to prefer waters of low salinity (<23‰). Dense populations were rarely found in the outer regions of the estuary.

Strong seasonal patterns were observed in the occurrence of *Calanus sinicus*. Dense populations were found only in January (Fig. 2.8). The population declined during spring and summer and no individual was found during autumn. *C. sinicus* showed strong preference for waters of high salinity and low temperature. Individuals were found in the inner stations only during winter when oceanic waters intruded into the inner estuary.

Strong seasonal pattern was also observed in *Eucalanus subcrassus* (Fig. 2.9). The species was uncommon in the estuary during winter, spring and summer, but appearred in large numbers during September and October. Maximum abundance of 302 ind. m^{-3} was recorded at S12 in September 1991. *E. subcrassus* was most common in the outer parts of the estuary. It was not found in the inner estuary (S1 to S5) during spring and summer and its density during autumn was higher in the outer than in the inner regions of the estuary. *E. subcrassus* occurred in very low numbers during winter. Fig. 2.13 shows that *E. subcrassus* was most abundant in temperatures around 28°C and salinity >25‰.

Fig. 2.10 presents the seasonal and spatial distribution of *Labidocera euchaeta* in the Zhujiang River estuary. *L. euchaeta* was one of the two species that occurred throughout the sampling period. No distinct seasonal pattern was observed. Densities >200 ind. m^{-3} were recorded in January 1992, April 1995 and October 1992. *L. euchaeta* occurred in low numbers during the other sampling cruises and was nearly

absent during July 1995 and July 1996. *L. euchaeta* (Fig. 2.13) occurred in temperatures ranging from 16 to 29.6°C and salinities from 2.5 to 36.0‰.

Paracalanus parvus was uncommon in the Zhujiang River estuary during 1991 and 1992 (Fig. 2.11). A dramatic increase in numbers occurred in 1995 when *P. parvus* formed 27.2% of the copepod community in January. *P. parvus* continued to occur in low numbers during the rest of 1995 and the first half of 1996. *P. parvus* seemed to prefer the outer regions of the estuary and was restricted to waters of salinity >10‰ (Fig. 2.13). Temperature for the occurrence of *P. parvus* ranged from 15.0 to 28.6°C (Fig. 2.13).

Strong seasonal and spatial patterns were found in the occurrence of *P. poplesia* (Fig. 2.12). Dense populations were found only during the spring. *P. poplesia* was always absent from the entire estuary during autumn (September and October). Spatial distribution of *P. poplesia* was confined to the inner regions of the estuary. Individuals were never found beyond S7. Fig. 2.13 shows that *P. poplesia* was most common in temperatures ranging from 18.8 to 22.6°C and salinities <10‰.

2.5 Discussion

The copepod community of the Zhujaing River estuary was made up of endemic estuarine species, coastal and/or oceanic species, and freshwater species. Most of the copepods found in the estuary were of coastal and/or oceanic origins. These species were carried into the estuary by coastal and oceanic currents, and were found mainly in the outer regions of the estuary during the dry season.

Calanoida was the most dominant zooplankton in the Zhujiang River estuary. Dominance of Calanoida has been reported in many other estuarine systems (Millar 1983; Taylor 1993; Gouda and Panigraphy 1995; Mishra and Panigraphy 1996). Among the 49 copepod species identified, 39 belonged to the Order Calanoida.

2.5.1 Seasonal variations in copepod abundance

Although copepod abundance (Fig. 2.4) in the Zhujiang River estuary showed no clear seasonal patterns, numbers were usually lower during the summer. The reason for that was not clear. In general, the zooplankton densities in estuarine environments increase during the summer (Mallin 1991; Sautour and Castel 1993; Lopes 1994) because the rate of reproduction increases with water temperature. In the Zhujiang River estuary, low densities in the summer may be related to the heavy freshwater outflow during the rainy season. Morton and Morton (1983) speculated that high mid-summer influx of freshwater from the Zhujiang River may inhibit the breeding activities of some zooplankton species. It was also reported by Leitao *et al.* (1992) that the zooplankton in the estuaries of the Massangana River and Tatuoca Suape River in Brazil was quantitatively poorer in the rainy season than in the dry

season. A distinct summer minimum for macrozooplankton (>500 μm) was also observed in Card Sound, an estuarine area in Biscayne Bay (Day *et al.* 1989).

Changes in copepod density in the Zhujiang River estuary was not related to variations in chlorophyll *a* concentration. According to Day *et al.* (1989), fluctuations in estuarine zooplankton abundance often did not follow changes in phytoplankton standing crop. Chlorophyll concentration also correlated poorly with copepod abundance in estuaries in North Carolina (Mallin 1991). Estuarine zooplankton is less dependent on phytoplankton than are oceanic species. Some workers have reported that suspended organic detritus and ciliates are important food sources for estuarine macrozooplankton (Robertson 1983; Day *et al.* 1989).

Copepod abundance was consistently low at high chlorophyll *a* concentration (>10 mg m^{-3}). As previously recorded in Tolo Harbour, Hong Kong, increase in chlorophyll *a* concentration was often caused by dramatic rise in abundance of bloom-forming dinoflagellates (Chan and Wong 1993). Some dinoflagellates contain no nutritional factors for survival and development of marine copepods (Huntley *et al.* 1987) and would not provide nutritional benefit to the copepod community. In addition, many zooplankton herbivores are known to avoid dense patches of dinoflagellates (Fiedler 1982).

2.5.2 Seasonal and spatial variations in species diversity

High species diversity was recorded in all the autumns and one of the winters (1996) during the course of this study. Oceanic influences are highest during the dry winter months when freshwater discharge from the Zhujiang River is at a minimum. As a result, copepods of oceanic and neritic origins enter the estuary with the intrusion of the oceanic water. It is well documented that the faunal assemblages endemic to estuaries are usually of lower diversity than those of oceanic and neritic origins (McLusky 1981). Chen (1982) also reported that the eastern and southern coasts of Hong Kong (South China Sea) show a greater species diversity of copepods than the mouth of the Zhujiang River estuary. Clearly, zooplankton diversity in the Zhujiang River estuary is also enriched by the intrusion of oceanic and neritic copepods during the dry autumn and winter months.

Increase in zooplankton diversity during the dry season has been recorded in the other studies. For example, the microzooplankton in the estuary of River Paripe, Brazil, was more diverse during the dry season (Leitao *et al.* 1996). In the Bathurst Harbour estuary in southwestern Tasmania, the plankton community contained very few taxa during the period of peak freshwater outflow (Edgar and Gresswell 1991).

The dominance of oceanic influence can also account for the higher species diversity recorded in the outer regions of the estuary, especially in stations S9 and S11. The outer regions of the estuary are influenced throughout the year by oceanic currents containing a high diversity of zooplankton. As a result, a more diverse community of coastal and oceanic copepods can be found in the outer regions of the Zhujiang River estuary.

Many authors have also reported that the outer regions of estuaries contained copepod communities of higher diversity and oceanic origin. In the Dharamtar creek adjoining Bombay harbour (India), Tiwari and Nair (1993) observed that a more diversified copepod assemblage of oceanic and neritic species characterized the lower estuarine zone with less salinity fluctuations. Kimmerer (1993) found that species in inner estuaries contained fewer species than outer estuaries where species came from nearby neritic waters. Similarly, a more oceanic composition of copepods was observed in the lower part of the Gulf of Nicoya and estuary on the Pacific coast of Costa Rica (Morales-Ramirez and Vargas 1995; Morales-Ramirez 1996).

Copepod species diversity was higher in S9 and S11 than in S10 and S12 although the stations were of relatively similar distance from the origin of freshwater discharge from the Zhujiang River. S10 and S12 receive a stronger freshwater influence from the river than S9 and S11 because flow from the river is diverted to the western part of the estuary by the earth's rotation (Chau 1961; McClimans 1988). Being less strongly influenced by oceanic waters, S10 and S12 contained fewer copepods of oceanic and neritic origin and lower species diversity when compared to S9 and S11.

2.5.3 Seasonal and spatial distribution of dominant species

Most estuarine zooplankton species have evolved broad physiological tolerances to ensure survival in the highly variable conditions of estuaries (Day *et al.* 1989). Most of the dominant copepods in the Zhujiang River estuary could be found in a wide range of salinity and temperature.

Acartia spinicauda and *Labidocera euchaeta* occurred perennially in the Zhujiang River estuary. *A. spinicauda* is commonly reported in coastal (Chen and Zhang 1965; Cheng *et al.* 1965; Gajbhiye *et al.* 1991; Yoo *et al.* 1991) and estuarine (Cheng *et al.* 1965; Tiwari and Nair 1993) environments. It is also a dominant copepod in other estuaries (Tiwari and Nair 1993). Seasonal shift in spatial distribution of *A. spinicauda* was observed. The population stayed in the inner estuary during winter and early-spring, migrated seaward during mid-spring and summer and moved back to the inner estuary in autumn. Temporal shift in spatial boundaries of copepods has been reported in the Westerschelde estuary in Belgium and the Netherlands (Soetaert and Van-Rijswijk 1993). Castel (1995) proposed that the movement of populations along the estuary was mainly governed by the seasonal change in river flow and salinity. Seasonal change in salinity may account for the movement of the *A. spinicauda* populations in the Zhujiang River estuary. *A. spinicauda* preferred brackish waters with salinities ranging from 10 to 24.5‰. During winter and early-spring, when river runoff was low and salinity was high in the entire estuary, *A. spinicauda* retreats to the inner estuary. During mid-spring and summer, the population was probably progressively transported to the outer estuary by freshwater discharge from the river. Salinity in the inner estuary was too low and the center of the population was displaced to the outer regions of the estuary. During

autumn when river discharge began to recede again, the outer estuary became too oceanic and *A. spinicauda* returned to the inner estuary.

Acartia spinicauda was previously reported by Chen (1982) near the Zhujiang River estuary. He noted that it contributed an important component of the zooplankton population in spring (April to May) and was most numerous towards the mouth of the Zhujiang River. In contrast, results presented here show that the number of *A. spinicauda* was very low near the river mouth in April. Difference in rainfall and river discharge may account for this difference. Chen (1982) also found that off the west coast of Lantau Island (near S11 in this study), abundance of *A. spinicauda* was very low (~2 ind. m^{-3}) during summer to early autumn (August to September). This is consistent with results of the present study.

Results of the present study show that *Labidocera euchaeta* is an euryhaline and eurythermal species. Perennial existence of *L. euchaeta* has been recorded in both the Zhujiang River estuary and a subtropical estuary in Xiamen of the Fujian Province (Lin and Li 1991; Yanyu *et al.* 1991). *L. euchaeta* is an estuarine species (Chen and Zhang 1965; Cheng *et al.* 1965; Lin and Li 1991; Suh *et al.* 1991; Yanyu *et al.* 1991; Chen 1992). It is eurythermal and occurs in low salinity coastal waters of the South China Sea (Cheng *et al.* 1965; Chen 1992).

Acartiella sinensis preferred the inner estuary and waters of lower salinity (<23‰). Yanyu *et al.* (1991) reported that *A. sinensis* is a low salinity estuarine species. It inhabits coastal waters, especially brackish waters near estuaries (Shen and Song 1979; Cheng *et al.* 1982). Occassionally, it may even appear in freshwater habitats (Shen and Song 1979). Previoulsy, *A. sinensis* has been reported in the estuarine regions of the Zhujiang River by Shen and Song (1979).

Seasonal occurrence of *Calanus sinicus* in the Zhujiang River estuary was strong. It was found in high abundance only during winter and spring. *C. sinicus* is a temperate species (Chen and Zhang 1965; Chen 1992) and is widely distributed in the Chinese coastal waters of Bohai, the Yellow Sea and the East China Sea (Chen and Zhang 1965), as well as around the Inland Sea of Japan (Huang *et al.* 1993) and Korea (Choi and Park 1993). As the optimal temperature for its reproduction is between 10 to 18°C (Chen 1992), *C. sinicus* probably reproduces throughout the year in temperate waters, as demonstrated by populations in the Kii Channel in the Inland Sea of Japan (Huang *et al.* 1993). In contrast, occurrence of *C. sinicus* in the South China Sea was strongly seasonal. In winter, the Taiwan Current flows along the coast of China from northeast to southwest (Chen 1992). Typical temperate nearshore species such as *C. sinicus* are carried along with the currents into the northern part of the South China Sea (Chen 1992). Because river runoff from the Zhujiang River was minimal during winter, *C. sinicus* is carried into the estuary by coastal currents. Abundance of *C. sinicus* in the Zhujiang River estuary was greatest during the winter. In January 1992, the population penetrated into the innermost stations of the estuary near the river mouth. Moreover, water temperature in the estuary during winter (~16°C) was suitable for the reproduction of *C. sinicus* (Chen 1992). During spring when river runoff and temperature start to increase and the influence of the northeast monsoon begins to drop, the number of *C. sinicus* decreased and the center of the population was displaced to the outer regions of the estuary. The distribution of *C. sinicus* showed strong spatial pattern. Densities were always higher in the outer than the inner regions of the estuary. *C. sinicus* preferred waters of high salinity and was rarely found in river mouth areas (Chen 1992).

Similar to *Calanus sinicus*, *Eucalanus subcrassus* is not endemic to estuarine environments but was carried into the Zhujiang River estuary seasonally by ocean currents. Seasonal pattern of occurrence was strong for the *E. subcrassus*. Density was extremely high during the autumn. Similar observation was reported by Chen (1992) for *E. subcrassus* in the pelagic and coastal regions of the South China Sea. Numbers were low from winter to summer and did not begin to increase until August. The maximum density of 50 ind. m^{-3} recorded by Chen (1992) was much lower than the 302 ind. m^{-3} recorded in this study.

Eucalanus subcrassus preferred temperatures around 28°C and salinity >25‰ (Fig. 2.13). *E. subcrassus* is a warm-water oceanic species (Cheng *et al.* 1965; Yanyu *et al.* 1991). Warm water temperature in summer and autumn favours the occurrence of *E. subcrassus* in coastal waters to the south of Hong Kong (Chen 1982). *E. subcrassus* appears in the coastal waters of the Fujian Province every summer because it was brought into the area by currents from the South China Sea. Density of *E. subcrassus* in the Zhujiang River estuary was low during early summer because the estuarine water was diluted by river discharge. In autumn, river runoff was reduced and *E. subcrassus* was carried into the estuary by warm currents from the South China Sea. Water temperature in the autumn was probably high enough for the reproduction of *E. subcrassus*. *E. subcrassus* was rare in the inner regions of the estuary because it was not well adapted to salinity <25‰.

Paracalanus parvus favoured salinity >10‰ and was most common in the outer regions of the Zhujiang River estuary. Similar finding has been reported by Millar (1983), Hulsizer (1976) and Ambler *et al.* (1985). *P. parvus* was common in the lower reaches of Australian estuaries where salinity was higher (Millar 1983). Similarly, *P. parvus* was found only in low numbers near the head of Narragansett

Bay (USA) where salinity was low (Hulsizer 1976). Ambler *et al.* (1985) reported that *P. parvus* was most abundant in waters of salinity >15 ‰. *P. parvus* is the dominant copepod in many marine coastal areas (Chen and Zhang 1965; Cheng *et al.* 1965; Park *et al.* 1991; Choi and Park 1993; Dias 1994; Lokman 1994; Gomez-Gutierrez *et al.* 1995). It is uncommon in low salinity areas such as the upper parts of the estuary near the mouth of river discharge. One exception was noted by Morales-Ramirez (1996) who regarded *P. parvus* as a neritic estuarine species which dominated the zooplankton community in the upper part of the Gulf of Nicoya, an estuary in the Pacific coast of Coasta Rica (Morales-Ramirez and Vargas 1995).

It should be noted that the abundance of *Paracalanus parvus* in the Zhujiang River estuary was extremely low during 1991 and 1992. Much higher densities were encountered in 1995 and 1996 and the species was reported to occur in the South China Sea in large numbers several decades ago by Chen and Zhang (1965).

The seasonal and spatial distribution of *Pseudodiaptomus poplesia* in the Zhujiang River estuary suggested that it is a warm water estuarine species which preferred waters of low salinity and temperatures ranging from 18.8 to 22.6°C. The seasonal pattern for the occurrence of *P. poplesia* was extremely strong. Dense populations were found only in spring. During the other seasons, *P. poplesia* was either extremely rare or even absent. The disappearance of *P. poplesia* from the planktonic population in the estuary may follow the formation of resting eggs which settled in bottom sediments during periods of unfavourable environmental conditions (Grice and Gibson 1975; Millar 1983). Re-occurrence of planktonic forms in the estuary was achieved by hatching of resting eggs. Temperature and salinity appear to be the dominant factors controlling the production and hatching of resting eggs

(Millar 1983). However, the production and hatching of resting eggs in *P. poplesia* have not been studied and further research is required to uncover this issue.

2.5.4 Seasonal succession and spatial segregation of dominant copepods

Both seasonal succession and spatial segregation were exhibited by the dominant copepods in the Zhujiang River estuary. *Calanus sinicus*, *Pseudodiaptomus poplesia* and *Eucalanus subcrassus* were seasonally separated from each other by dominating the planktonic community at different times of the year. These species are considered to be temporary inhabitants of the estuary as they tended to disappear totally from the planktonic assemblage during particular seasons. Species that occurred in the estuary at the same time exhibited spatial segregation by occupying different parts of the estuary. The seasonal and spatial occurrence of the dominant species was probably determined by the seasonal variations in temperature and longitudinal salinity gradient in the estuary (Diouf and Dialls 1990; Lopes 1994; Palomares-Garcia and Gomez-Gutierrez 1996).

Seasonal succession and spatial segregation of copepods in estuaries have previously been studied. For example, alternation between domination by *Acartia clausi* and *Acartia tonsa* had been reported in some estuaries on the east coast of North America (Millar 1983). In a hypersaline estuary in southern Senegal, 3 species of *Acartia* (*A. plumosa*, *A. clausi* and *A. grani*) showed a temporal and spatial succession of dominance (Diouf and Dialls 1990). Salinity and/or temperature determined the dominant species. Lopes (1994) showed that indigenous estuarine copepod species were spatial segregated from the marine euryhaline species in the estuary of the Guarau River in southeastern Brazil. Estuarine copepods dominated the upper estuary while the marine euryhaline species were more common in the lower estuary. Similar observations have been reported by Millar (1983) in the estuary of the St. Lawerence River.

2.5.5 Seasonal and spatial distribution of non-dominant copepods

Acrocalanus gibber, *Canthocalanus pauper*, *Euchaeta concinna* and *Temora turbinata* belonged to a group (Subgroup 1) which showed strong seasonal and spatial patterns of occurrence. Both *A. gibber* and *C. pauper* occurred only in the outer estuary during autumn. *A. gibber* has been reported from coastal (Cheng *et al.* 1965; Tiwari and Nair 1993) and oceanic waters of China and other parts of the world (Cheng *et al.* 1965; Nair *et al.* 1989). Large numbers are found during autumn in the coastal water of Fujian. *C. pauper* is a tropical (Chen and Zhang 1965) neritic (Morales-Ramirez 1996) species. It has been reported from various coastal (Cheng *et al.* 1965; Chen 1982) and oceanic (Chen and Zhang 1965; Cheng *et al.* 1965) waters. It is most common in salinities ranging from 31.0 to 33.0‰ (Chen 1992). It appeared in large numbers during summer and autumn in the South China Sea and reached peak density in October (Chen 1992). In Xiamen Harbour in southern China, the highest density of *C. pauper* was recorded in autumn (Cheng *et al.* 1965). *C. pauper* is also a dominant copepod in coastal waters to the south of Hong Kong and occurs in large numbers during winter in the west of Lantau Island near S11 in this study (Chen 1982). These results suggest that *A. gibber* and *C. pauper* are not endemic to the Zhujiang River estuary but were transported seasonally into the estuary from nearby coastal waters by ocean currents.

Euchaeta concinna and *Temora turbinata* occurred only during autumn and winter in the outer parts of the Zhujiang River estuary. Both copepods prefer waters of high salinity (Chen 1992; Björnberg 1971; Chisholm and Roff 1990). *E. concinna* preferred salinities ranging from 33 to 34‰, while *T. turbinata* preferred salinities ranging from 31 to 33‰ (Chen 1992). Although *E. concinna* was described as an

offshore species by Chen (1992), it has been reported from coastal waters of China and many parts of the world (Chen and Zhang 1965; Cheng *et al.* 1965). *T. turbinata* has been found in both inshore (Björnberg 1971) and offshore (Chen 1992) waters. In addition, it occurs in various coastal (Chen and Zhang 1965; Cheng *et al.* 1965; Chisholm and Roff 1990; Yanyu *et al.* 1991; Nomura and Murano 1992; Roff *et al.* 1995; Goswami and Padmavati 1996; Hwang and Turner 1995) and oceanic water bodies (Chen and Zhang 1965; Cheng *et al.* 1965; Roff *et al.* 1995). According to Chen (1982), *E. concinna* and *T. turbinata* were dominant copepods in coastal waters to the south of Hong Kong during both summer and autumn. Dense populations of both species have been found off the western coast of Lantau Island (near S11 in this study) during winter (Chen 1982).

Although *Temora turbinata* and *Canthocalanus pauper* have been found to occur in large numbers during the summer in high salinity coastal waters near the Zhujiang River estuary (Chen 1982), neither species were found inside the estuary. Low salinity probably excluded *T. turbinata* and *C. pauper* from the Zhujiang River estuary during the summer.

Unlike the group of species mentioned above, *Centropages tenuiremis* and *Tortanus forcipatus* was found throughout the estuary during winter and spring. The species has been described as neritic and estuarine by Cheng *et al.* (1965) and as low salinity neritic by Yanyu *et al.* (1991). The lack of spatial preference suggests that *C. tenuiremis* adapts to a wide range of salinity. *C. tenuiremis* is common in subtropical estuaries (Yanyu *et al.* 1991). It is also abundant in the mesohaline zones (~28‰) of the estuaries of the Mankyoung River and Dongjin River (Suh *et al.* 1991). *T. forcipatus* is a coastal copepod (Millar 1983). It occurs in great numbers in waters around Fujian during the autumn. In the estuarine systems of the Mankyoung River

and Dongjin River, *T. forcipatus* occurred only in waters of 28‰ salinity (Suh *et al.* 1991).

A third group of species showed clear spatial preference but exhibited no seasonal pattern of occurrence. Among the 8 species belonging to this group, 7 preferred the outer estuary and were rarely found in low salinity waters in the inner estuary. *Candacia* sp. is a tropical species (Chen and Zhang 1965) found in both coastal (Chen and Zhang 1965; Go *et al.* 1996) and oceanic (Chen and Zhang 1965; Kang and Hong 1995) waters of the world. In estuarine environments, it is restricted to the outer regions. Morales-Ramirez (1996) found that the oceanic species *Candacia catula* occurred mostly in the outer parts of the Golfo Dulce estuary.

Species belonging to the genus *Euchaeta* are exclusively coastal (Bollens and Frost 1991; Oreland 1991; Park *et al.* 1991; Hong *et al.* 1994) and oceanic (Mauchline 1992; Mauchline 1995; Oresland 1995; Roff *et al.* 1995; Albers *et al.* 1996; Hays 1996) in origin. *Euchaeta marina* is a well-known oceanic (Björnberg 1971) and offshore (Cheng *et al.* 1965) species. It has been reported in oceanic waters around China (Cheng *et al.* 1965; Chen 1992) and various parts of the world (Gomez-Gutierrez and Hernandez-Trujille 1994; Kouwenberg 1994; Roff *et al.* 1995). In addition, it has also been found in the coastal waters of southern China (Chen and Zhang 1965; Chen 1992), northwestern Mediterranean (Kouwenberg 1994) and Jamaica in West Indies (Roff *et al.* 1995).

Paracalanus aculeatus is a tropical copepod (Cheng *et al.* 1965; Chisholm and Roff 1990). It is described as oceanic by Björnberg (1971) and Morales-Ramirez (1996) and as neritic by Chisholm and Roff (1990). It has been found in the coastal waters of China, including the South China Sea (Chen and Zhang 1965; Cheng *et al.* 1965; Lokman 1994) and many parts of world including the Gulf of Mexico

(Checkley *et al.* 1992b), Jamaica (Chisholm and Roff 1990) and Japan (Cheng *et al.* 1965). In the Golfo Dulce estuary, it is restricted to the outer regions where oceanic influence dominates (Morales-Ramirez 1996).

Temora discaudata is regarded as a neritic (Cheng *et al.* 1965; Chen and Zhang 1965; Arcos and Fleminger 1991) species and is usually found in coastal waters. It has a worldwide distribution and, in China, has been reported from the coastal waters of Fujian and Zhejiang (Chen and Zhang 1965).

Undinula vulgaris is a tropical species (Cheng *et al.* 1965; Chen 1992). It is oceanic (Björnberg 1971) and favours waters of high salinity (33-34‰) and temperatures ranging from 21.7 to 28.7°C (Chen 1992). Occurrence in coastal areas is also common for this species. It has been reported from coastal waters off Fujian and Zhejiang in summer and autumn (Chen and Zhang 1965) and southern Hong Kong in winter (Chen 1982).

Paracalanus crassirostris was the only species which preferred the inner regions of the Zhujiang River estuary and showed no seasonal pattern of occurrence. Densities up to 11 ind. m^{-3} were recorded at S2 and S4. *P. crassirostris* is neritic in nature (Cheng *et al.* 1982) and often exists in great numbers in estuaries (Chen and Zhang 1965; Leitao *et al.* 1992), coastal inlets (Gajbhiye *et al.* 1991) and harbours (Chen and Zhang 1965; Kim and Lee 1994). Although it has been considered a high salinity species by Björnberg (1971), previous study by Chen (1982) suggested that *P. crassirostris* was most numerous towards the mouth or (inner area) of the Zhujiang River estuary where salinity was low.

A number of species in the Zhujiang River estuary did not show any discernible tendency in spatial and temporal distribution. The lack of spatial pattern suggests that most of these species are euryhaline neritic species. For example,

Calanopia thompsoni is a subtropical neritic species (Cheng *et al.* 1965) which can live in waters of low salinity (Yanyu *et al.*1991; Chen 1992). It is commonly found in subtropical estuaries and low salinity waters in the South China Sea (Yanyu *et al.*1991).

Labidocera bipinnata is a neirtic species which exists in large numbers in estuarine waters (Cheng *et al.* 1965). This species has been found in the estuarine systems of the Mankyoung River and Dongjin River (Suh *et al.* 1991).

Labidocera pavo has been reported from coastal waters around China and Japan (Chen and Zhang 1965). Large numbers have been found in low salinity waters in many harbours (Cheng *et al.* 1965).

Tortanus dextrilobatus and *Tortanus gracilis* are common in low salinity estuarine waters, although dense populations have been found in some coastal areas (Chen and Zhang 1965; Cheng *et al.* 1982). *T. dextrilobatus* has been described as a low salinity estuarine species by Yanyu *et al.* (1991) and as a coastal species by Chen (1992). It usually inhabits areas near river mouths (Yanyu *et al.* 1991) and has been found in brackish waters in South Korea (Ohtsuka *et al.* 1992) and in low salinity coastal waters of Fujiang and Xiamen in southern China (Chen and Zhang 1965; Chen 1992). *T. gracilis* is common in the estuarine and nearshore waters along the coast of China (Cheng *et al.* 1982).

Corycaeus affinis is an indicator species of coastal waters (Kang *et al.* 1990). Its distribution ranges from brackish estuarine waters (Suh *et al.* 1991; Chen 1992) and coastal waters (Chen *et al.* 1974; Choi and Park 1993) to oceanic waters (Lee *et al.* 1993). Specimens have been collected in the brackish northwestern part of Deep Bay (close to S6 and S9 in this study) in spring by Chen (1992).

Oithona occurs mainly in coastal (Nomura *et al.* 1992; Kim and Lee 1994; King and Williamson 1995; Morales-Ramirez 1996) and oceanic (Fernandez *et al.* 1993; Boettger-Schnack 1994; Hillgruber *et al.* 1995; Errhif *et al.* 1997) waters of high salinity. *O. rigida* is a neritic species that lives in the surface water (Cheng *et al.* 1965). It has been found offshore in Zhejiang, Fijian and the South China Sea. *O. rigida* and *Oithona* sp. were probably transported into the inner parts of the Zhujiang River estuary by tidal currents.

A total of 14 species occurred only once in outer regions of the Zhujiang River estuary during autumn and winter. Most were of neritic and oceanic origins. These species appeared in the outer regions of the estuary only during the dry season when freshwater discharge from the Zhujiang River was low and oceanic water intruded extensively into the estuary.

Acartia danae is a tropical neritic species (Cheng *et al.* 1965; Chen and Zhang 1965). It has been found in the coastal waters of Fujian and Zhejiang in the autumn (Chen and Zhang 1965). Outside China, it has been found in different bay areas in Korea (Yoo *et al.* 1991) and coastal waters of Japan (Cheng *et al.* 1965) and Mexico (Gomez-Gutierrez *et al.* 1995).

Candacia simplex is a tropical species and has been found in the offshore waters of Zhejiang during the autumn (Chen and Zhang 1965).

Centropages orsinii is an offshore species (Cheng *et al.* 1965). It appears in oceanic waters off Zhejiang during the autumn (Chen and Zhang 1965; Cheng *et al.* 1965). Outside China, it has been reported from Japan, Malaysia, Australia, the Pacific Ocean, the Indian Ocean and the Red Sea (Chen and Zhang 1965; Cheng *et al.* 1965).

Clasocalanus furcatus has been found in the coastal waters of China (Chen and Zhang 1965), Japan (Cheng *et al.* 1965), the Gulf of Mexico (Checkley *et al.* 1992a) and Jamaica (Roff *et al.* 1995). In Jamaica, it has been found in both coastal and oceanic waters (Roff *et al.* 1995).

Labidocera acuta is a tropical species (Cheng *et al.* 1965) found most commonly in coastal waters (Chen and Zhang 1965; Cheng *et al.* 1965; Hernandez-Trujillo 1989). In China, it occurs in the autumn in the coastal waters of Zhejiang and Fujian (Chen and Zhang 1965).

Four species of *Corycaeus* were recorded only once. *C. catus*, *C. crassiusculus*, *C. speciosus* are inhabitants of warm-oceanic waters (Kang *et al.* 1990). *C. catus* has been found in the offshore waters of Zhejiang and oceans all over the world (Chen *et al.* 1974). *C. crassiusculus* and *C. speciosus* are common in the coastal waters of the South China Sea (Chen *et al.* 1974). *C. dahli* is common in both nearshore and offshore environments (Chen *et al.* 1974; Cheng *et al.* 1982).

Oithona decipiens is common in the coastal waters of the South China Sea (Chen *et al.* 1974). *Oithona venusta* is most commonly found in coastal waters (Chen *et al.* 1974; Hirakawa *et al.* 1990; Chen 1982; Hwang and Turner 1995; Roff *et al.* 1995; Go *et al.* 1996), although its occurrence in oceanic waters has also been reported (Roff *et al.* 1995). In estuarine environments, it is restricted to areas where oceanic conditions dominate (Han *et al.* 1991; Morales-Ramirez 1996).

Among the 14 species with single occurrence, 3 were found in low salinity waters. *Acartia erythraea* was described as a low-salinity species by Chen (1992) and has been found in the coastal waters from southern China to Korea (Chen and Zhang 1965; Cheng *et al.* 1965; Yoo *et al.* 1991). *Pontellopsis regalis* and *Pontellopsis tenuicauda* have been found in estuaries (Cheng *et al.* 1965; Cheng and Zhang 1965),

coastal waters (Chen and Zhang 1965; Checkley *et al.* 1992b; Baessa-de-Aguiar 1991), as well as open oceans (Cheng *et al.* 1982; Chen and Shen 1974).

Some freshwater copepods can extend their distribution into brackish waters (Millar 1983). Dense populations of freshwater species often appear in estuaries after periods of heavy river flow (Cronin *et al.* 1962). The freshwater species *Heliodiaptomus falxus*, *Neodiaptomus schmackeri, Phyllodiaptomus tunguidus* and *Sinocalanus sinensis* appeared in the upper parts of the Zhujiang River estuary during the rainy season. *H. falxus*, *N. schmackeri* and *P. tunguidus* belong to the successful and widespread freshwater family Diaptomidae (Reddy 1994). *H. falxus* and *P. tunguidus* have previously been found in the deltaic regions of the Zhujiang River (Shen and Song 1979; Dumont and Reddy 1993; Reddy 1994). *N. schmackeri* has been reported from freshwater habitats such as rivers, lakes, ponds, bogs and ricefields in southern China and Korea (Shen and Song 1979; Chang and Kim 1986; Bhattacharya *et al.* 1990). *S. sinensis* has been found in rivers, lakes, ponds, bogs and ricefields in Korea (Chang and Kim 1986). According to Shen and Song (1979), *S. sinensis* could also be found in brackish waters in many parts of China.

2.6 Conclusion

In conclusion, the structure of the copepod community in the Zhujiang River estuary was largely affected by the seasonal changes in physical environmental parameters such as temperature, salinity, freshwater outflows and ocean currents.

Seven species of calanoid copepods were considered dominant. All dominant species tended to be eurythermal and euryhaline, although each species had its own optimal range of temperature and salinity. Seasonal succession and spatial segregation were exhibited by some of the dominant copepods.

The 49 species identified in the copepod community came from several origins. Most species were derived from coastal and oceanic waters. Some species were endemic estuarine species adapted to brackish waters, while others were of freshwater origin.

The abundance of copepods did not show clear seasonal patterns, although the numbers were always lower in the summer. Species diversity was higher in the outer than in the inner regions of the Zhujiang River estuary. Most of the species found in the outer estuary were of coastal and/or oceanic origin and were transported into the estuary by ocean currents.

Chapter 3. Spatial and temporal distribution of marine cladocerans in Tolo Harbour, Hong Kong

3.1 Literature review

3.1.1 Geographical and seasonal distribution of marine cladocerans

Cladocerans (Subclass Branchiopoda, Order Cladocera) are small microcrustaceans. About 600 species have been described (Schram 1986), but the validity of some named taxa at the species level is somewhat debatable (Korovchinsky 1996). Most cladocerans live in freshwater. Species diversity in the marine envrionment is low (Cheng and Cao 1987). Marine cladocerans are cladocerans that live in estuaries, inland mesohaline or hyperhaline water systems, neritic waters, continental shelf waters and open oceans (Egloff *et al.* 1997). Of all the cladocerans that have been described, only eight species are distributed widely in both neritic and oceanic waters and can be considered as truly marine (Onbé 1977; Egloff *et al.* 1997). Using the classification of Egloff *et al.* (1997), the eight species are *Penilia avirostris*, *Evadne nordmanni*, *Evadne spinifera*, *Pseudevadne tergestina*, *Podon intermedius*, *Podon leuckarti*, *Pleopis polyphemoides* and *Pleopis schmackeri*. With the exception of *P. avirostris*, which belongs to the Family Sididae, all species are classified under the Family Podonidae. *P. polyphemoides* was formerly placed under the genus *Podon*, while *P. tergestina* was formerly classified as *Evadne tergestina* (Egloff *et al.* 1997).

Compared to marine copepods, marine cladocerans have received far less attention from plankton biologists largely due to their sporadic occurrence and low

species diversity in the sea. Some investigators, however, have recognized that marine cladocerans have a nearly worldwide distribution in both coastal waters and open oceans (Cheng and Cao 1987; Yoo and Kim 1987; Kim and Onbé 1995). In addition, marine cladocerans have been observed to constitute a significant portion of the zooplankton in many coastal and estuarine regions of temperate and tropical seas, especially during the summer (Onbé 1977; Park *et al.* 1991; Bochdansky and Hernade 1992; Nomura and Murano 1992; Gislason and Astthorsson 1995). A number of recent studies (Onbé 1977; Turner *et al.* 1988; Cai 1990) have shown that marine cladocerans may play an important role in the trophic dynamic of the marine food web.

Some marine cladocerans have a worldwide distribution in both coastal and oceanic waters. For example, *Penilia avirostris* has been reported from the coastal waters of Korea (Yoo and Kim 1987), various parts of China (Cheng and Cao 1987; Cai 1990; Chen and Huang 1992; Tang *et al.* 1995), Japan (Onbé 1977; Mullin and Onbé 1992; Onbé and Ikeda 1995), Jamaica (Webber *et al.* 1996), the northwestern Mediterranean Sea (Pagano *et al.* 1993), the Black Sea (Bologa *et al.* 1995), southern Brazil (Rocha 1985), western Nigeria (Egborge *et al.* 1994), Chile (Mujica and Espinoza 1994) and various parts of North America (Bosch and Taylor 1967; Conley and Turner 1991; Checkley *et al.* 1992b). The distribution of *P. avirostris* in the northeastern Pacific extends from coastal to open oceanic waters (Kim and Onbé 1995).

Evadne nordmanni has been found in the coastal waters of Korea (Yoo and Kim 1987), northern China (Cheng and Cao 1987), Japan (Onbé 1977; Onbé and Ikeda 1995), the North Sea (Jorgensen 1933), Chile (Mujica and Espinoza 1994), southwestern Iceland (Gislason and Astthorsson 1995) and Canada (Brown and

Gaskin 1989). The species has also been reported from both the coastal and oceanic waters of the north Atlantic (Gieskes 1971a). *Evadne spinifera* has been reported from the coastal region of Korea (Kim *et al.* 1993a), the southern Japan Sea (Onbé and Ikeda 1995), the northwestern Mediterranean Sea (Pagano *et al.* 1993), the Black Sea (Bologa *et al.* 1995), the coastal waters of Chile (Mujica and Espinoza 1994), southern Brazil (Rocha 1985) and the north Atlantic (Gieskes 1971a). The species is also common in the open oceanic waters of the eastern Pacific (Longhurst and Seibert 1972; Schram 1986) and the north Atlantic (Gieskes 1971a). *Pseudevadne tergestina* occurs in the coastal waters of Korea (Yoo and Kim 1987), China (Cheng and Cao 1987), Japan (Onbé 1977; Mullin and Onbé 1992; Onbé and Ikeda 1995), western Nigeria (Egborge *et al.* 1994), Chile (Mujica and Espinoza 1994), southern Brazil (Rocha 1985), the Texas coast of the Gulf of Mexico (Checkley *et al.* 1992b) and the eastern Pacific (Longhurst and Seibert 1972).

Among podonids, *Podon intermedius* occurs in the coastal waters of Japan (Onbé 1977), Chile (Mujica and Espinoza 1994), the Canary Islands (Lozano-Soldevilla and Rodriguez 1994), the North Sea (Jorgensen 1933; Gieskes 1971b) and both the coastal and open waters of the north Atlantic (Gieskes 1971a). *Podon leuckarti* is common in the seas around Japan (Onbé 1977; Onbé and Ikeda 1995) and Korea (Yoo and Kim 1987). In addition, occurrence has been reported from the North Sea (Gieskes 1971b), the north Atlantic (Gieskes 1971a) and seas to southwest of Iceland (Gislason and Astthorsson 1995). *Pleopis polyphemoides* occurs in the coastal waters of Korea (Yoo and Kim 1987), northern China (Cheng and Cao 1987), Japan (Onbé 1977), the North Sea (Jorgensen 1933), the northwestern Mediterranean Sea (Pagano *et al.* 1993), the west coast of Sweden (Turner and Granéli 1992), the Chesapeake Bay (Bosch and Taylor 1967) and the north Atlantic (Gieskes 1971a).

Pleopis schmackeri has been known to exist in the coastal waters of Vietnam (Kim and Onbé 1989a), China (Cheng and Cao 1987), Korea (Kim and Onbé 1989a), Japan (Onbé 1983; Onbé and Ikeda 1995), the Caspian Sea (Aladin 1995), Brazil (Rocha 1985) and the northwest Pacific (Kim and Onbé 1989a, b).

Marine cladocerans form an important component of the zooplankton in surface waters around Hong Kong and the northern parts of the South China Sea. Five species, including *Penilia avirostris* (Chen 1982; Cai 1990; Angelino and Della Croce 1992; Chen and Huang 1992; Wong *et al.* 1992a; Tang *et al.* 1995), *Evadne nordmanni* (Angelino and Della Croce 1992), *Pseudevadne tergestina* (Chen 1982; Cai 1990; Chen and Huang 1992; Angelino and Della Croce 1992; Tang *et al.* 1995), *Podon leuckarti* (Angelino and Della Croce 1992) and *Pleopis schmackeri* (Cheng and Cao 1987; Cai 1990; Chan 1991; Chen and Huang 1992; Angelino and Della Croce 1992; Tang *et al.* 1995) have been recorded.

While reports of seasonal occurrence and geographical distribution suggest that most marine cladocerans are euryhaline and eurythermal, each species has its optimal range of salinity and temperature. *Penilia avirostris*, *Pleopis polyphemoides*, *Podon leukarti*, *Pseudevadne tergestina* and *Evadne nordmanni* are inhabitants of neritic waters (Gieskes 1971b; Onbé 1977; Bryan 1979; Gislason and Astthorsson 1995), although oceanic occurrence of *P. tergestina* has been reported by Longhurst and Seibert (1972). *Pleopis schmackeri* prefers distant neritic environment and *Evadne spinifera* is common in oceanic environment (Gieskes 1971a; Kim *et al.* 1993a). *Podon intermedius* shows no preference and can be found in both neritic and oceanic environments (Gieskes 1971b). *P. avirsotris*, *P. intermedius, P. schmackeri*, *P. tergestina* and *E. spinifera* prefer warmer waters (Gieskes 1971b; Onbé 1977; Bryan 1979; Kim and Onbé 1989a; Cheng and Cao 1987) than *P. polyphemoides*, *P.*

leuckarti and *E. nordmanni* (Gieskes 1971a, b; Onbé 1977; Kim *et al.* 1993a; Gislason and Astthorsson 1995).

Temporal variation in the abundance of marine cladocerans is great with marked seasonality (Bainbridge 1958; Gieskes 1971b; Onbé 1978; Onbé 1985; Yoo and Kim 1987; Cai 1990; Chen and Huang 1992). Numerical dominance is usually recorded during the summer when water temperature is high. In temperate waters, disappearance from the zooplankton community occurs in winter when temperature is low and food is rare (Bainbridge 1958; Geiskes 1971a; Onbé 1977; Onbé 1985; Yoo and Kim 1987; Chen and Huang 1992; Jorgensen 1933). *Penilia avirostris* exists in the zooplankton throughout the year in some subtropical regions and exhibits marked numerical peak during the summer (Cai 1990; Tang *et al.* 1995).

Seasonal succession is a common phenomenon in marine cladocerans. The congeneric species *Podon leuckarti* and *Pleopis schmackeri* did not co-exist in time in the southern Japan Sea (Onbé and Ikeda 1995). Seasonal successions of *Pseudevadne tergestina* by *Evadne nordmanni* and *Pleopis polyphemoides* by *P. leuckarti* have been observed in the central part of the Inland Sea of Japan (Onbé 1977). *P. leukarti* was replaced by *Podon intermedius* when water became warmer in the North Sea (Gieskes 1971b).

3.1.2 Vertical distribution

3.1.2.1 Diel vertical migration

Diel vertical migration (DVM) by crustacean zooplankton has been studied extensively in both marine (Enright 1977; Cervetto *et al.* 1993; Huang *et al.* 1993; Tang *et al.* 1994) and freshwater (Weider 1984; Dodson 1988; Ringelberg *et al.* 1991;

Young and Watt 1993; Brancelj and Blejec 1994; Angeli *et al.* 1995; Makino *et al.* 1996) systems. Most populations exhibit 'nocturnal' (or 'normal') DVM by migrating upward from deeper waters at dusk, staying near the surface during part or most of the night, and returning to deeper strata at dawn.

Because DVM is energy consuming (metabolic disadvantage) and has been shown (e.g. Lampert 1989) to prolong egg development time when the females are in the colder and deeper waters (i.e. demographic disadvantage), adaptive advantages driving its occurrence must be present for migratory behaviour to be widespread among zooplankters. Hypotheses related to factors such as demographic advantages (McLaren 1974), starvation avoidance (Geller 1986), metabolic advantages (Enright 1977) and avoidance of ultra-violet (UV) radiations (Bollens and Frost 1990) have been proposed. However, each hypothesis has its own drawbacks (see review by Lampert 1993). For example, the hypotheses suggested by Geller (1986) and McLaren (1974) cannot explain the timing of DVM. The metabolic advantages proposed by Enright (1977) is not in concordance with observations in nature (Lampert 1989). Protection from UV-light damage does not require the deep migration exhibited by many species because UV is already absorbed in the uppermost part of the water column even in clear open oceans.

In contrast to the hypotheses mentioned above, hypotheses related to avoidance of visual predation in the surface water are most widely accepted by planktologists (Ringelberg *et al.* 1991; Haney 1993; Loose 1993; Herwig and Schindler 1996). In the majority of cases, the visual predators are planktivorous fish, although surface-orienting aquatic insects such as *Notonecta* which feed at the surface water may impose similar selective pressure on zooplankton as those of planktivorous fish in some freshwater systems (Scott and Murdoch 1983; Dodson and Havel 1988;

Herwig and Schindler 1996). For example, the freshwater cladoceran *Daphnia hyalina* started vertical migration with the appearance of the juvenile perch *Perca fluvitalitis* in the open water of Lake Maarsseveen (Ringelberg *et al.* 1991). Similarly, daphnids in some fishless small ponds performed normal DVM in the presence of surface-orienting planktivorous aquatic insects (Herwig and Schindler 1996).

The visual predation avoidance hypothesis can explain the timing of DVM. Moreover, it is consistent with the prediction that the more conspicuous zooplankton such as large and pigmented individuals and egg-carrying females are more easily detected by predators and are likely to perform more pronounced vertical migration (Enright and Honegger 1977; Stuart and Pillar 1990; Huang *et al.* 1993; Lampert 1993; Morales *et al.* 1993; Brancelj and Blejec 1994; Angeli *et al.* 1995; Makino *et al.* 1996).

Some findings suggest that diel vertical migration is a dynamic rather than a fixed, invariant behaviour (Ohman 1990; Levy 1990). For example, a fjord population of *Pseudocalanus newmani* expressed differential migration behaviour ranging from normal DVM to no migration or even reverse DVM under different predatory pressures in Dabob Bay (Ohman 1990). In many cases, DVM behaviour seemed to be flexible and could be induced by proximate cues such as light (Loose 1993; Ringelberg 1993), temperature (Haney 1993; Young and Watt 1993), food concentration (Haney 1993), toxins released by cyanobacteria (Berthon and Brousse 1995; Fradkin and Gilbert 1996) and chemical exudates released by predators (Neill 1990; Larsson and Dodson 1993).

Reverse DVM with nocturnal descent is exhibited by some zooplankters (Onbé 1977; Ohman *et al.* 1983; Levy 1990; Neill 1990; Onbé and Ikeda 1995), although it is not as common as normal DVM. Reverse DVM may serve as a defense mechanism

against non-visual invertebrate predators which perform normal DVM and is not contradictory to the predation avoidance hypothesis (Lampert 1993). For example, *Daphnia* exhibited reverse DVM to avoid the invertebrate predator *Chaoborus* which performed normal DVM (Cooper 1983; Herwig and Schindler 1996). The freshwater calanoid copepod *Diaptomus kenai* exhibited reverse migration when it was exposed to *Chaoborus* or water previously containing *Chaoborus* (Neill 1990). Similarly, the small marine copepod *Pseudocalanus* sp. exhibited reverse migration to avoid predation by non-visual feeding invertebrate predators *Sagitta elegans*, *Euchaeta elongata* and *Euphausia pacifica* which showed normal DVM (Ohman *et al.* 1983).

Some zooplankters undergo reverse migration as they themselves may be visual predators. Marine cladocerans such as *Evadne* and *Pseudevadne* have been known to exhibit pronounced reverse migration (Onbé and Ikeda 1995). These marine cladocerans have well-developed compound eyes and may move to the surface water in daytime to feed visually on motile tintinnids and dinoflagellates (Bainbridge 1958; Cheng and Cao 1987).

3.1.2.2 Marine cladocerans as epiplankters

Cladocerans are regarded as epiplankters because they occur mostly in the surface water (Cheng and Cao 1987). A typical example to demonstrate the surface-dwelling characteristic of cladocerans is that the freshwater cladoceran *Daphnia galeata* is restricted mostly to the upper 15 m in Lake Ros (Gliwicz and Rykowska 1992). Marine cladocerans are also epiplankters. *Pseudevadne tergestina* and *Penilia avirostris* are most abundant in the upper 10 m in the Inland Sea of Japan and the Gulf of Mexico (Mullin and Onbé 1992). *Evadne nordmanni* is rare in depth >35 m in the

Northumbrian Sea (Jorgensen 1933). *P. tergestina* and *Evadne spinifera* restrict their distribution in the eastern Pacific to not lower than 20 m (Longhurst and Seibert 1972). *E. nordmani* and *Podon leuckarti* are most common in the surface layers in waters of southwestern Iceland (Gislason and Astthorsson 1995).

3.1.2.3 Diel vertical distribution of marine cladocerans

Vertical migration behaviour has been widely reported in both freshwater (Lampert 1987; Dini and Carpenter 1991; Loose 1993; Brancelj and Blejec 1994; Herwig and Schindler 1996; Makino *et al.* 1996) and marine cladocerans (Onbé 1977; Mullin and Onbé 1992; Wong *et al.* 1992b; Pagano *et al.* 1993; Onbé and Ikeda 1995). Onbé and Ikeda (1995) found that some marine cladocerans exhibited reverse DVM by staying near the surface during the day and migrating to deeper waters at night. Reverse DVM is especially common among marine podonids (Onbé 1977). Examples of reverse DVM have been reported for *Pleopis polyphemoides* in the Inland Sea of Japan (Onbé 1977) and the northwestern Mediterranean Sea (Pagano *et al.* 1993), *Pleopis schmackeri* in the southern Japan Sea (Onbe and Ikeda 1995), *Pseudevadne tergestina* in the Inland Sea of Japan and the southern Japan Sea (Onbé 1977; Mullin and Onbé 1992; Onbé and Ikeda 1995), and *Evadne nordmanni* and *Evadne spinifera* in the southern Japan Sea (Onbé and Ikeda 1995). Different patterns of DVM have been observed in *Penilia avirostris*. The species did not show significant DVM in the seas around Japan (Onbé 1977; Onbé and Ikeda 1995), but performed normal DVM in Tolo Harbour of Hong Kong (Wong *et al.* 1992b). Reverse DVM was exhibited by *P. avirostris* in the northwest Mediterranean Sea (Pagano *et al.* 1993).

Size variations in vertical distribution have not been studied extensively in marine cladocerans. Most examples in the literatures are from freshwater species. The

larger individuals or adults of *Daphnia longispina* (Hanazato *et al.* 1989) and *Daphnia hyalina* x *galeata* hybrid (DeMeester *et al.* 1995) were found in deeper strata than the smaller individuals or juveniles in daytime. Watt and Young (1992) reported that *Daphnia magna* exhibited size variations in vertical distribution during both day and night. In most cases, the behaviour could be attributed to the need to avoid predation by planktivorous fish (Hanazato *et al.* 1989; DeMeester *et al.* 1995). Among marine cladocerans, large individuals of *Pseudevadne tergestina* were found deeper in the water column than the smaller individuals, especially at night (Mullin and Onbé 1992).

3.1.3 Horizontal distribution

Horizontal distribution of marine cladocerans was usually described in large geographical scales (Longhurst and Seibert 1972; Yoo and Kim 1987; Kim *et al.* 1993a; Gieskes 1971b; Tang *et al.* 1995). Small scale inshore-offshore horizontal distribution has rarely been studied. An example of marine cladocerans showing patchiness over small horizontal distances was documented in *Evadne nordmanni* by Jorgensen (1933). The animals seeked shallow coastal waters during the asexual phase when parthenogenetic broods were being produced, remained in shallow regions until pairing had taken place and resting eggs had formed, and subsequently returned to deeper waters (Jorgensen 1933).

Compared to marine species, small scale horizontal distribution is well documented among freshwater cladocerans. Shore-avoidance behaviour (Gliwicz and Rykowska 1992; Taleb *et al.* 1994; Visman *et al.* 1994) occurs when the distribution of cladocerans shows offshore-inshore gradients in density, usually with a dramatic decrease in density towards the inshore region of the lake. Large species or more

conspicuous individuals of the same species avoid the inshore region by staying in the deeper pelagial area. As a result, the inshore population tends to consist of smaller individuals (Gliwicz and Rykowska 1992; Taleb *et al.* 1994; Visman *et al.* 1994; Koksvik 1995). Such shore avoidance behaviour may be illumination-induced (Gliwicz and Rykowska 1992). Higher predation risk in the well-illuminated littoral zone imposed by visual predators such as planktivorous fish may be the selective force for such behaviour (Gliwicz and Rykowska 1992; Visman *et al.* 1994; Taleb *et al.* 1994).

Shore-aggregation occurs when macrophytes in the inshore regions act as shelter and provide hiding places for cladocerans to escape from predators (Davies 1985; DeMeester *et al.* 1993; Kvam and Kleiven 1995). *Scapholeberis mucronata* aggregated in the well-vegetated littoral zone of a small eutrophic pond during daytime to avoid predation by planktivorous fish (DeMeester *et al.* 1993). Dense swarms of *Daphnia longispina* remained around the vegetative littoral region of Lake Myravatn to avoid the invertebrate predator *Chaoborus* which preferred to stay offshore (Kvam and Kleiven 1995).

3.1.4 Reproduction

The reproductive biology of marine cladocerans was recently reviewed by Egloff *et al.* (1997). Specifically, the life cycle of marine cladocerans consists of an asexual phase (parthenogenesis) and a sexual phase (gamogenesis). Parthenogenesis allows cladoceran populations to increase rapidly under favourable conditions (Onbé 1977). Paedogenesis is a kind of parthenogenesis in which advanced embryos in the brood pouch already contain their own embryos in their embryonic brood spaces.

Paedogenesis has been documented in all seven species of marine podonids (Kim and Onbé 1989a). Gamogenesis, typified by the appearance of males and females with resting eggs, occurs when stressful environmental conditions cause the population to decline (Onbé 1977). Resting eggs produced may sink to the bottom and serve as 'seed population' for the resurgence of the next planktonic population (Onbé 1985).

Brood maturation in parthenogenetic females of marine cladocerans seems to be triggered by darkness (Bryan 1979; Mullin and Onbé 1992). For example, parthenogenetic females of *Pseudevadne tergestina* in the Inland Sea of Japan (Mullin and Onbé 1992) and the Chesapeake Bay (Bryan 1979) bear embryos with pigmented eyes at night and release them before dawn. Similarly, *Penilia avirostris* females, which can carry mature eyed-embryos during both day and night, are most likely to be gravid at night in both the Japan Sea and the Gulf of Mexico (Mullin and Onbé 1992).

3.1.5 Feeding

3.1.5.1 Food composition

Most freshwater cladocerans are suspension feeders of algae (deBernardi *et al.* 1987; Manca and deBernardi 1987; Tóth *et al.* 1987; Boersma and Vijverberg 1995; Trubetskova and Lampert 1995). In addition to algae, herbivorous cladocerans may also feed on bacteria, protozoa and detritus (Cheng and Cao 1987; Tóth *et al.* 1987).

Predatory feeding occurs in freshwater cladocerans such as *Leptodora* and *Bythotrephes* (deBernardi *et al.* 1987). These predatory cladocerans prey on other smaller herbivorous cladocerans such as *Daphnia* and *Diaphanosoma* (DeStasio *et al.* 1995; Herzig 1995; Lehman and Cáceres 1993), although copepods and rotifers are also consumed (Cummins *et al.* 1969; Edmonson and Litt 1987; Lunte and Luecke

1990). Both *Leptodora* and *Bythotrephes* posses well-developed compound eyes and strong appendages to facilitate the searching and handling of prey (Mordukhai-Boltovskoi 1968; Schram 1986; Herzig 1995). Monakov (1972) reported that *Leptodora* tore their prey with their mandibles and then sucked in the food.

Among marine cladocerans, *Penilia avirostris* is a suspension feeder which ingests small food particles (Pavlova 1959; Cheng and Cao 1987; Kim *et al.* 1989) using feeding appendages in the form of fine meshes (Turner *et al.* 1988). The major food items include diatoms and dinoflagellates (Kim *et al.* 1989, 1993a; Kim and Onbé 1989a). *P. avirostris* may also feed on bacteria (Pavlova 1959; Paffenhöfer and Orcutt 1986) and detritus (Pavlova 1959). Turner *et al.* (1988) pointed out that *P. avirostris* may not be a bacterivore which feed on bacteria directly. Instead, it feeds on bacterivorous microflagellates and serves as an important component of the "microbial loop" between the bacterioplankton and higher consumers.

Marine podonids are usually regarded as raptorial and predatory feeders (Bainbridge 1958; Mordukhai-Boltovskoi 1968; Gieskes 1971b; Schram 1986; Cheng and Cao 1987; Jagger *et al.* 1988). They adopt a predatory mode of life by possessing huge eyes and powerful grasping mouthpart appendages and legs for catching movable prey (Bainbridge 1958; Mordukhai-Boltovskoi 1968).

'Motile' dinoflagellates are long believed to be the major food items of marine podonids (Bainbridge 1958; Morey-Gaines 1979; Jagger *et al.* 1988; Turner and Granéli 1992; Onbé and Ikeda 1995). Bainbridge (1958) observed the capture of dinoflagellates *Peridinium*, *Gonyaulax* and *Certaium* by *Evadne nordmanni*. The presence of the thecae of *Ceratium* in the gut of *Pleopis polyphemoides* (Morey-Gaines 1979) and *Gonyaulax excavata*, a toxic dinoflagellate, in the gut of *E. nordmanni* (White 1980) indicate that dinoflagellates were eaten by marine podonids.

Turner and Granéli (1992) also reported that *P. polyphemoides* ingested various dinoflagellates. The association of dense populations of *P. polyphemoides* with *Certaium* blooms provides further indirect evidence for the trophic relationship between marine podonids and dinoflagellates (Morey-Gaines 1979). Kim *et al.* (1993b) reported that weakly motile flagellates such as *Prorocentrum micans* and *Protoperidinium* sp. were eaten by *E. nordmanni, Pseudevadne tergestina, Podon leuckarti* and *P. polyphemoides*. Motile organisms such as athecate microflagellates and tintinnids were also considered to be the food of *P. polyphemoides* (Turner and Granéli 1992) and *E. nordmanni* (Bainbridge 1958), respectively.

Kim *et al.* (1989) observed that marine podonids preferred immotile organisms and materials to active and motile organisms. Onbé and Ikeda (1995) found that immotile centric diatoms were grazed by marine podonids. Turner and Granéli (1992) observed that *Pleopis polyphemoides* ingested various diatoms. Kim *et al.* (1989), according to SEM observation of gut contents, reported that the food items of *Evadne nordmanni, Pseudevadne tergestina, Podon leuckarti* and *P. polyphemoides* were largely confined to centric diatoms, although a more recent study by Kim *et al.* (1993b) revealed that motile flagellates were also ingested. In some studies, detrius has been found to be an important food source for marine podonids (Conover 1978; Cheng and Cao 1987).

3.1.5.2 Diel feeding behaviour

Diel feeding rhythms have been widely reported for both marine (Fuller 1937; Gauld 1953; Mackas and Bohrer 1976; Head *et al.* 1985; Dagg *et al.* 1989; Wong *et al.* 1990; Tang *et al.* 1994) and freshwater (Lampert and Taylor 1985; Angeli *et al.*

1995; Makino *et al.* 1996) zooplankton. In most cases, feeding activity was found to be greater at night (Starkweather 1983; Chisolm *et al.* 1975; Mackas and Bohrer 1976; Dagg *et al.* 1989; Tang *et al.* 1994; Angeli *et al.* 1995; Makino *et al.* 1996). Angeli *et al.* (1995) reported that the gut fullness of *Daphnia* was 14 times higher at night than during the day in Lake Geneva (France). Similarly, *Daphnia longispina* and *Bosmina coregoni* in Lake Toya (Japan) showed clear feeding rhythm by having significantly more gut pigments at night than during the day (Makino *et al.* 1996).

Although nocturnal feeding was common among crustacean zooplankton, daytime feeding and absence of feeding rhythm have also been reported (Mackas and Bohrer 1976; Dagg and Wyman 1983; Welschmeyer *et al.* 1984; Dagg and Walser 1987; Atkinson *et al.* 1992). For example, Chow-Fraser and Knoechel (1985) reported that there was no significant difference between the day and night feeding rates of *Bosmina,* while Persson (1985) reported that the feeding activity of *Bosmina* was most intense during the day.

Some authors (Gauld 1953; Hart 1977) proposed that diel feeding rhythm is caused by DVM as the animals moves in and out of the food-rich surface layer in a stratified water body. While coupling between DVM and feeding patterns have been recorded in field studies (Haney and Hall 1975; Lampert and Taylor 1985; Dini *et al.* 1987; Geller *et al.* 1992), lack of association between DVM and feeding rhythm is also common in both marine and freshwater zooplankton (Angeli *et al.* 1995). Diel feeding rhythms may occur in the absence of DVM (Fuller 1937; Mackas and Bohrer 1976; Head *et al.* 1985; Peterson *et al.* 1990; Tang *et al.* 1994; Makino *et al.* 1996) and in homogenous food conditions (Dawidowicz and Loose 1992; Dam and Peterson 1993). Nocturnal feeding may start before the onset of nocturnal DVM (Tang *et al.* 1994; Angeli *et al.* 1995). Dagg *et al.* (1989) reported that active feeding by

zooplankton began only after sunset even though the animals have already arrived at the food-rich upper water before sunset. Makino *et al.* (1996) observed that *Daphnia longispina* stayed in the relatively dense food layers during the whole day, but fed actively only at night.

Feeding rhythms appear to be related to the light-dark cycle and are not necessarily associated with DVM (Makino *et al.* 1996). Many observations indicate that nocturnal feeding is independent of DVM and diel changes in the gut pigments reflect actual changes in feeding intensity. Recent studies of crustacean zooplankton demonstrate that the diel feeding rhythm and DVM are controlled independently by light (Head *et al.* 1985; Stearns 1986; Dagg *et al.* 1989; Makino *et al.* 1996). Light may act as an exogenous factor to induce changes in feeding behaviour (Makino *et al.* 1996). High light intensity may inhibit the feeding activities of marine copepods (Head *et al.* 1985; Stearns 1986). Feeding rhythms may also be under endogenous control as both marine and freshwater zooplankton continue to exhibit feeding rhythms in constant darkness (Starkweather 1983; Duval and Geen 1976; Stearns 1986). Some observations suggest that light may act as a powerful 'zeitgeber' to control the endogenous diel feeding activity of zooplankton (Head *et al.* 1985; Stearns 1986; Dagg *et al.* 1989).

Predator avoidance is believed to be one of the ultimate causes for the nocturnal feeding behaviour of zooplankton. Dagg *et al.* (1989) suggested that feeding activity of the migratory *Calanus pacificus* was confined to nocturnal hours to reduce the risk of detection by visual planktivores. Feeding zooplankters may attract visual predators by their foraging movements and guts packed with food may enhance visibility (Dagg *et al.* 1989). Mourelatos *et al.* (1989) also proposed that reduction of feeding activity by zooplankton during daytime may serve to minimize the risk of fish

predation. The body pigmentation of zooplankton increases with feeding activity (Kleppel *et al.* 1985). Nocturnal feeding may be a mechanism to prevent the accumulation of body pigments which attract visual predators in daytime (Kleppel *et al.* 1985).

3.1.6 Site description of Tolo Harbour

Tolo Harbour is a sea inlet in the northeastern part of Hong Kong. It consists of a shallow inner harbour which opens into the Mirs Bay and the South China Sea through a narrow tidal channel (Tolo Channel). The entire inlet has an area of about 50 km^2. The total length is approximately 16 km. The width varies from about 5 km in the inner harbour to just over 1 km at the mouth. As Tolo Harbour is nearly land-locked and partially enclosed, tidal exchange rates is poor (Trott and Fung 1973). Water residence time is between 16 to 42 days (Oakley and Cripps 1972; Preston 1975). The overall range of tidal levels in Tolo Harbour is 0.1 to 2.7 m. Tolo Harbour has an average depth of 10.9 m (Trott 1973) and a maximum depth of about 22 m (Wear *et al.* 1984). The bottom of Tolo Harbour is nearly level and covered by a layer of fine silt and clay (Oakley and Cripps 1972). Tolo Harbour is an important breeding and feeding ground for a wide variety of marine fishes.

Water temperature in Tolo Harbour is strongly influenced by air temperature. Summer temperature ranges from 27 to 31°C at the surface and falls to between 17 to 29°C at the bottom, while winter temperature ranges from 15 to 19°C (Chan 1991). During summer, the water column is vertically stratified (Wear *et al.* 1984; Lam and Ho 1989; Chan 1991; Tang 1993). A thermocline forms in April and breaks in October (Wear *et al.* 1984; Chan 1991).

Salinity in Tolo Harbour ranges from 13.9 to 38‰ (Trott 1973; Kueh 1974; Chan 1991). Marked seasonal variation in salinity exists (Wear *et al.* 1984; Kueh 1974). Water is generally more saline during the dry winter and spring than during the rainy summer and early autumn (Kueh 1974). A halocline is usually present during the rainy season from May to the end of September (Wear *et al.* 1984; Lam and Ho 1989).

The surface water of Tolo Harbour is often characterized by supersaturation (>100% saturation) of dissolved oxygen (Oakley and Cripps 1972; Kueh 1974; Wear *et al.* 1984; EPD 1986; Chan 1991; Tang 1993) caused by excessive algal growth (EPD 1986). In summer when the thermocline (Wu 1988; Chan 1991; Tang 1993) and halocline are prominent (Wu 1988), oxygen difference between the surface and bottom is great. Wind-driven vertical mixing occurs after the thermocline breaks down in late autumn and dissolved oxygen in the bottom layer increases (Wear *et al.* 1984; Tang 1993).

In general, water becomes clearer and less eutrophic towards the mouth of the harbour (Trott 1973; Trott and Fung 1973; Chan 1991). Visibility is higher in summer than in winter because the sea is calmer and bottom sediments are less disturbed during summer (Wear *et al.* 1984; Tang 1993).

Chlorophyll *a* level in offshore oceanic waters is generally less than 2 ng mL^{-1} (EPD 1987). Tolo Harbour is considered eutrophic because annual mean chlorophyll *a* concentration in the surface water is often higher than 10 ng mL^{-1} (EPD 1990). In general, chlorophyll *a* concentration is highest in the inner harbour and decreases slightly towards the channel (Wear *et al.* 1984; Chan and Hodgkiss 1987; Chan 1991). Algal blooms are most common during the spring and chlorophyll *a* concentration is usually higher in the summer than in the winter (Chan 1991).

3.2 Introduction

Marine cladocerans are common in both coastal and open oceans, yet information on their biology and ecology is rather scarce. Previous studies of marine cladocerans have focused on their geographical distribution (Jorgensen 1933; Bosch and Taylor 1967; Gieskes 1971a, b; Longhurst and Seibert 1972; Brown and Gaskin 1989; Kim *et al.* 1993a; Tang *et al.* 1995; Webber *et al.* 1996), seasonal occurrence (Jorgensen 1933; Gieskes 1971a, b; Yoo and Kim 1987; Brown and Gaskin 1989; Kim *et al.* 1993a; Egborge *et al.* 1994; Gislason and Astthorsson 1995; Tang *et al.*1995), reproductive biology, diet and life history (Jorgensen 1933; Onbé 1977; Bryan 1979; Onbé 1985; Paffenhöfer and Orcutt 1986; Turner *et al.* 1988; Kim and Onbé 1989a; Marcus 1990; Tang *et al.* 1995; Egloff *et al.* 1997). Very few studies have been conducted on the temporal and spatial distribution of marine cladocerans over short time periods and short distances. Reports of vertical migration patterns varied from no migration to reverse diel vertical migration (Onbé and Ikeda 1995; Mullin and Onbé 1992).

The aim of this study is to provide information on the behaviour and ecology of marine cladocerans in Tolo Harbour, Hong Kong. The specific objectives are: 1) to study diel change in vertical and horizontal distribution among marine cladocerans, 2) to study diel change in their feeding intensity, and 3) to investigate the relationship between vertical migration and diel feeding rhythm.

3.3 Materials and methods

3.3.1 Field sampling

The study was carried out in Tolo Harbour (Fig. 3.1) on 23 May 1996. Samples were collected during the day between 1250 and 1630 h and at night between 2110 and 2250 h. Night sampling began approximately two hours after the sunset. Nine sampling stations were spaced out along a horizontal transect from inshore to offshore (Fig. 3.1).

Distance between adjacent stations was about 30 m. The position of each station was marked by a buoy. Water depth was greatest at the outermost station (S1) and decreased towards the shore. In daytime, water depth at the 9 sampling stations ranged from 21 m in S1, the outermost station, to 3.5 m in S9, the innermost station. Water depth at the sampling stations decreased at night due to tidal difference and slight shift in the position of sampling stations, as the buoys were moved by strong winds and tidal currents. Water depth at S1 and S9 were 17 m and 2 m respectively. Sampling was carried out as rapidly as possible to minimize temporal variations in spatial distribution and grazing intensity of zooplankton. Hydrographical parameters were measured simultaneously to zooplankton sampling.

3.3.1.1 Physical parameters

Physical parameters including temperature, dissolved oxygen, salinity, turbidity, light intensity, current direction, wind speed and wind direction were measured at each sampling station. Vertical profiles of temperature and dissolved oxygen were measured with an electronic oxygen meter (YSI model 57) at 2 m

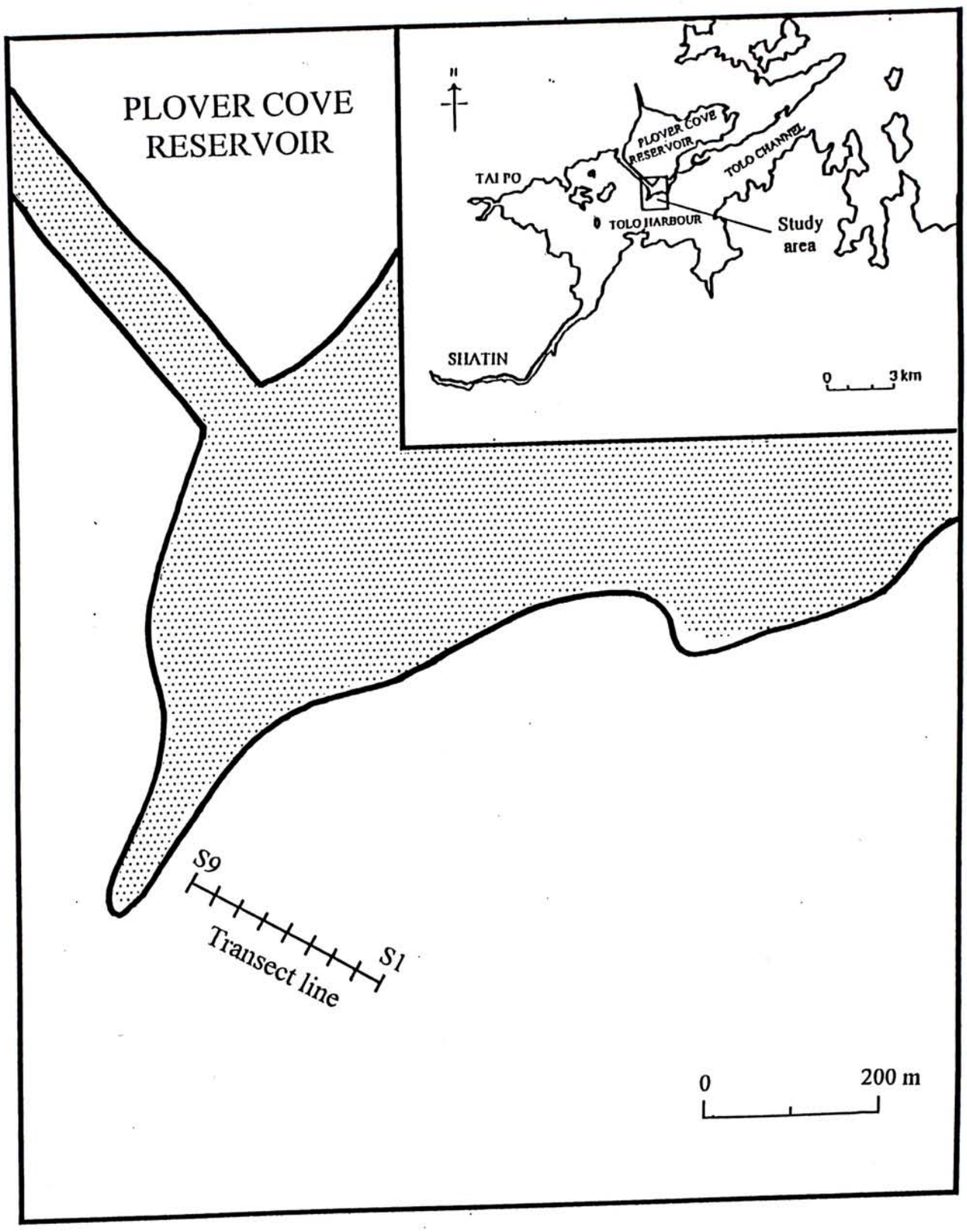


Fig.3.1 Map of Tolo Harbour (Hong Kong) showing the position of 9 sampling stations along the horizontal transect.

intervals. Water samples collected with a Van Dorn water sampler at 2 m intervals were measured for salinity with a refractometer. Turbidity was estimated using a 0.35 m diameter Secchi disk. Light intensity was measured with a LI-190 SA Quantum sensor while wind speed was recorded with an electronic wind speed indicator (Davis Instruments). The direction of wind and surface current was recorded visually. Most physical parameters were measured during both day and night. Turbidity was measured only in daytime and salinity was recorded only at night.

3.3.1.2 Ambient chlorophyll concentration

Ambient chlorophyll *a* concentration at each sampling station was measured during both day and night. Water samples were collected with a Van Dorn water sampler from the middle of each depth stratum from which zooplankton samples were collected (e.g. at 2 m if zooplankton samples were hauled from 4 m to the surface). For each water sample, duplicate 10 mL subsamples were filtered through 0.45 μm Millipore membrane filters. Each filter was put into a Petri dish, wrapped with aluminum foil and returned to laboratory in a cooler packed with dry ice. In the laboratory, the amount of chlorophyll *a* on each filter was measured fluorometrically (Parson *et al.* 1984) using a Turner Designs 10 fluorometer.

3.3.1.3 Zooplankton sampling

Zooplankton was collected by making vertical hauls with a closing conical net (0.304 m mouth diameter, 125 μm mesh size). At S1, zooplankton samples were collected from 0-4 m, 4-8 m, 8-12 m and 12 m to 1 m above the bottom. At S2, zooplankton samples were collected from 0-4 m, 4-8 m and 8 m to 1 m above the

bottom. At S3, S4 and S5, zooplankton was collected from 0-4 m and 4 m to 1 m above the bottom. Water depth at the inshore sampling stations, S6, S7, S8 and S9, were less than 8 m, and zooplankton samples were collected by hauling the net from 1m above the bottom to the surface. In total, 17 cross-sectional zooplankton samples were collected from 9 sampling stations during both day and night.

Duplicate vertical hauls were made from each depth stratum. Zooplankton collected from the first haul was poured into a plastic bottle and preserved in 12% formalin immediately for enumeration in the laboratory under a stereomicroscope. Zooplankton collected from second haul was collected on a piece 125 μm-mesh nylon netting and transferred to a Petri dish. Liquid nitrogen was then poured over the Petri dish immediately to freeze the zooplankton. This procedure minimized the chance of gut pigment loss due to defecation by the animals. The Petri dishes were wrapped with aluminium foil and returned to the laboratory in a cooler packed with dry ice for analysis of gut pigment content.

3.3.1.4 Gut pigment content

The fluorometric method was used to determine the amount of chlorophyll derived pigments in the gut of marine cladocerans. Gut pigment content represented the amount of chlorophyll derived pigments in the guts of animals at the time of capture. The amount of chlorophyll *a* in the gut was small, phaeopigments (phaeophorbide and phaeophytin) usually made up >85% of the total pigment measured and only a small amount of chlorophyll was not digestively degraded (Dagg and Wyman 1983). Gut pigment content per individual was defined as the amount of chlorophyll *a* and phaeopigments in the gut.

Marine cladocerans were picked under a stereomicroscope and transferred to glass tubes containing 5 mL of 90% acetone for extraction overnight at 4°C in a dark refrigerator. Picking was carried out under low light intensity to minimize photo-degradation of gut pigments. Depending on availability, each glass tube contained up to 15 animals and duplicates were used whenever possible. Fluoroscence of each extracted sample was measured before and after acidification using a Turner Designs 10 fluorometer. Chlorophyll *a* and phaeopigments per individual were calculated from the equations of Dagg and Wyman (1983):

$$\text{ng chlorophyll ind.}^{-1} = K(R_b-R_a)v/n$$

$$\text{ng phaeopigments ind.}^{-1} = K(AR_a-R_b)v/n$$

where K is the machine calibration constant, R_b and R_a are the fluorescence reading before and after acidification, A is the acidification ratio, v is the volume of acetone extract and n is the number of cladoceran in the sample. Phaeopigments values were corrected for pigment destruction using an estimated average loss of 33% suggested by Dam and Peterson (1988). No correction was made for background fluoroscence following the suggestion of Wong *et al.* (1992a).

3.3.2 Measurement of gut evacuation rate

Gut evacuation rate was measured on shipboard on 12 March 1997. The experiment was carried out in daytime (1100 h) because it was impractical to conduct the experiment in a small boat at night.

Three vertical hauls from 10 m to the surface were made to collect enough animals for the experiment. Animals collected inside the cod end of the plankton net was immediately concentrated on a 125 μm mesh nylon sieve, washed gently with 0.45 μm Millipore filtered seawater, and transferred into a small bucket (~20 L) with

a porous bottom made of 125 μm mesh size netting. The small bucket was suspended in a much larger bucket (~80 L) containing 40-50 L of 0.45 μm Millipore-filtered seawater. The volume of seawater in the small bucket was maintained at around 16 L. The animals were contained inside the small bucket, but faecal materials smaller than 125 μm could pass through the sieve. Previous observations suggested that the gut pigment content of copepods did not decrease after the first 5 to 10 minutes because of ingestion of faecal materials (C. K. Wong, per. comm.). This method reduced the amount of faecal materials available to the experimental animals.

Evacuation rate was determined by monitoring the decrease in gut pigment content in starving animals. Animals were removed at the start of the experiment and after 2, 4, 6, 8 10, 15, 20, 30, 45, 61 and 90 minutes by filtering a small volume of seawater from the small bucket through a 125 μm nylon mesh. Seawater removed from the bucket during sampling was replaced immediately by fresh 0.45 μm filtered seawater.

Zooplankton collected on the nylon netting was transferred to a Petri dish and killed with liquid nitrogen. The Petri dishes were wrapped with aluminium foil and transferred to the laboratory in a cooler packed with dry ice for gut pigment analysis.

3.3.2.1 Gut evacuation rate

Cladocerans were sorted under a stereomicroscope. Gut pigment content of the animals was measured using procedures mentioned above. Gut pigment content was assumed to decline exponentially with time (Dagg and Wyman 1983; Chan 1991). Gut evacuation rates were calculated from the equation:

$$G_t = G_0 e^{-Rt}$$

where G_0 is the initial level of gut pigment content, G_t is the level of gut pigment content at time t and R is the instantaneous evacuation rate with units of min^{-1}.

3.3.2.2 Clearance rate

Gut evacuation rate can be used to convert gut pigment content to ingestion rate if ingestion is assumed to be, on average, equal to egestion (evacuation). Ingestion rate per individual (I) was calculated from the equation:

$$I \text{ (ng pigment } min^{-1} \text{ ind.}^{-1}) = RG$$

where R is the instantaneous gut evacuation rate constant (min^{-1}) and G is the level of gut content per individual (ng pigment $ind.^{-1}$).

Clearance rate (F) is defined by Frost (1972) as the volume of water processed per individual per day (mL $ind.^{-1}$ day^{-1}) and is calculated by the equation:

$$F = 24 \times 60 \times I/C$$

where C is the chlorophyll concentration (ng Chl mL^{-1}).

3.3.3 Zooplankton distribution

3.3.3.1 Quantitative analysis

Marine cladocerans preserved in 12% formalin were identified to species level according to Gieskes (1971c), Onbé (1983), Cheng and Cao (1987) and Kim and Onbé (1989a, b). Four species of marine cladocerans: *Pseudevadne tergestina* (Plate 3.1), *Penilia avirostris* (Plate 3.2), *Podon* sp. (Plate 3.3A) and *Pleopis schmackeri* (Plate 3.3B) were identified. Morphologically, *Podon* sp. is very similar to *P. schmackeri*, but *P. schmackeri* has a more rounded body outline, a shallower cervical

Plate 3.1 Morphology of *Pseudevadne tergestina* without eyed-embryo (A) and with eyed-embryos (B) observed under light microscope. Each scale bar represents 100 μm.

Plate 3.2 Morphology of *Penilia avirostris* without embryo (A), with small embryos (B) and with large embryos (C) observed under light microscope. Each scale bar represents 100 μm.

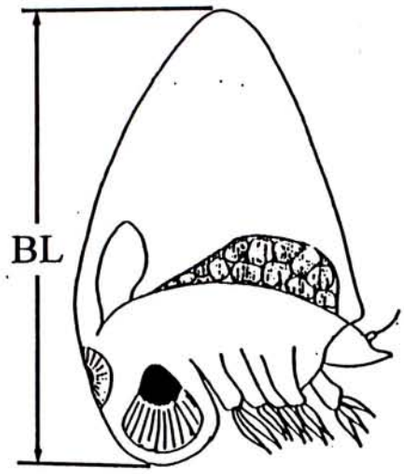
Plate 3.3 Morphology of *Podon* sp. (A) and *Pleopis schmackeri* (B) observed under light microscope. Each scale bar represents 100 μm.

groove, and a slenderer and more sharply pointed mucro (Onbé 1983) compared to *Podon* sp.

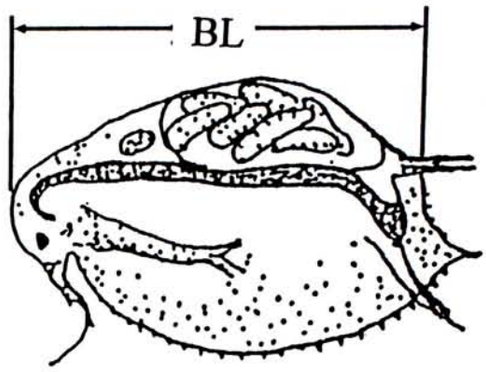
Density of each species in each sample was estimated by counting two subsamples representing at least 10% of the whole sample under a stereomicroscope. Density was expressed in number of individuals per cubic meter (ind. m^{-3}).

Body size was chosen to represent the maximum visual dimension perceived by visual predators. For each species, up to 20 individuals were randomly selected from each sample and sized under a stereomicroscope equipped with an ocular micrometer. Body size of *Penilia avirostris* (Fig. 3.2) was measured from the tip of the head to the end of the carapace before the mucro. Body sizes of podonids were measured as the maximum distance from the tip of the head to the dorso-posterior edge of the brood pouch (Fig. 3.2). This measurement was equivalent to the gross length mentioned in Onbé (1983).

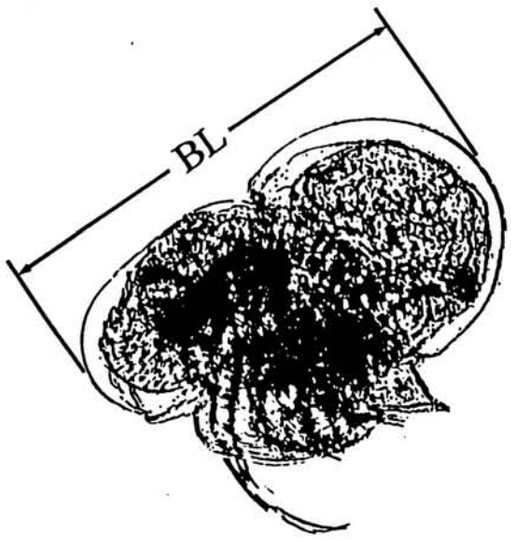
The reproductive conditions of *Penilia avirostris* and *Pseudevadne tergestina* were examined. Reproductive conditions of parthenogenetic females of *Penilia avirostris* were classified according to Onbé (1978) into those containing: 1) no embryo (no parthenogenetic egg), 2) small embryos (development stage I or II), and 3) large embryos (development stage III or above). Females at each reproductive condition are presented in Plate 3.2. Parthenogenetic eggs at stages I and II show no structural differentiation. Eggs at stage I are nearly spherical in shape. A stage II egg is different from a stage I egg by having a realm of depression around the upper portion. Embryos at stage III contain a pair of second antennae on the side of the body. Reproductive stages of *Pseudevadne* sp. were arbitrarily classified into those without embryo or without eyed-embryo and those with eyed-embryos as illustrated in Plate 3.1. Up to 50 females of each species were randomly selected from each sample. The proportion of females in each reproductive stage was determined, and the



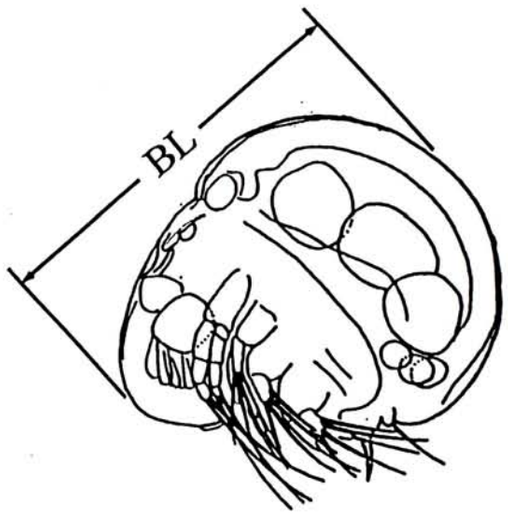
Pseudevadne tergestina



Penilia avirostris



Podon sp.



Pleopis schmackeri

Fig.3.2 The body length (BL) measurement of *Pseudevadne tergestina, Penilia avirostris, Podon* sp. and *Pleopis schmackeri.*

data were converted to densities by multiplying the proportion by the total density of females in each sample.

The reproductive conditions of *Podon* and *Pleopis schmackeri* were not studied because the density in most samples was too low for such an analysis.

3.3.4 Statistical analysis

3.3.4.1 Overall population

For each species of marine cladoceran, mean density at each sampling station is determined for both day and night. Mean densities at each of the 5 deep offshore stations (S1 to S5) represented the average of densities from different depths, while mean densities at each of the 4 shallow inshore stations (S6 to S9) represented densities estimated from single net haul from bottom to surface. The presence of diel change in population densities was tested by comparing mean densities at the 9 sampling stations during day and night by the paired-sample *t* test.

Two criteria were adopted to test for the presence of vertical migration. A population was considered to have performed either normal or reverse DVM when at least one of the two criteria was fulfilled. The first criterion was that the mean depths of the population at the 5 offshore stations (S1 to S5) differed significantly between day and night according to the paired-sample *t* test. The second criterion was that the percentage of population at the surface strata (0-4 m) of the 5 offshore stations differed significantly between day and night according to the paired-sample *t* test. For each station, percentage at the surface layer was calculated by dividing the number of animals collected at the surface by the total number of animals collected from the

entire water column sampled. This value was affected by the distribution of animals along the water column, but not by the total number of animals found.

Horizontal movement in each species of marine cladoceran was investigated by using the paired-sample *t* test to compare the percentages of the entire population at each of the 4 inshore stations (S6 to S9) between day and night. The percentage of the entire population at each inshore station was calculated by dividing the number of animals collected in that inshore station by the total number of animals collected from all 9 stations. Animals were regarded as performing diel horizontal migration if percentages of the entire population at the 4 inshore stations differed significantly between day and night.

All percentage data were arcsine transformed to obtain an underlying distribution that is more nearly normal (Zar 1996). A significant level of P=0.05 was used for all statistical tests. The directional nature of shift of population was not revealed by the statistical methods chosen but can be easily determined by inspection of data. The same approach was used for statistical analyses in the following sections.

3.3.4.2 Size

For each species of marine cladoceran, the presence of diel change in body size was tested by comparing the mean sizes at the 9 sampling stations during day and night using paired-sample *t* test.

Changes in body size along the water column were analyzed by comparing the mean body size of animals in the surface water (0-4 m) and in the bottom water (4 m to ~1 m above bottom) at the 5 offshore stations (S1 to S5) during day and night using the paired-sample *t* test. Data for day and night were analyzed separately.

Horizontal changes in body size was analyzed by comparing the mean body size at the 5 offshore stations (S1 to S5) to mean body size at the 4 inshore stations (S6 to S9) using the two-sample *t* test. Data for day and night were analyzed separately.

3.3.4.3 Reproductive condition

For *Penilia avirostris*, mean percentages of females at each of the 3 reproductive stages at each sampling station were determined for both day and night. Mean percentage at each of the 5 deep offshore stations (S1 to S5) represented the average of percentages from different depths, while mean percentage at each of the 4 shallow inshore stations (S6 to S9) represented percentage estimated from a single bottom-to-surface net haul. Diel changes in the proportion of females at each reproductive stage was tested by comparing the mean percentages at 9 sampling stations between day and night using paired-sample *t* test.

For *Penilia avirostris* females of each reproductive stage, two criteria were adopted to test for the presence of vertical migration behaviour. DVM, either normal or reverse, was considered to have occurred when at least one of the two criteria was met. The first criterion was that the mean depths of the population at the 5 offshore stations (S1 to S5) differed significantly between day and night according to the paired-sample *t* test. The second criterion was that the percentages of population at the surface layers (0-4 m) of the 5 offshore stations differed significantly between day and night according to the paired-sample *t* test. For each station, percentage at the surface stratum was calculated by dividing the total number of animals collected from the entire water column sampled.

Horizontal movements among *Penilia avirostris* females of a specific reproductive stage was investigated by using the paired-sample *t* test to compare the percentages of the population at the 4 inshore stations (S6 to S9) between day and night. The percentage at each inshore station was calculated by dividing the number of females at a specific reproductive stage collected in that inshore station by the total number of females at that reproductive stage collected from all 9 stations. Females of a specific reproductive stage were regarded as performing diel horizontal migration if percentages of the entire population at the 4 inshore stations differed significantly between day and night. Diel differences in the reproductive status of *Pseudevadne tergestina* were not treated statistically because females with eyed-embryos were found only at night.

3.3.4.4 Gut pigment content and gut clearance rate

The presence of diel change in gut pigment content of *Penilia avirostris* and *Pseudevadne tergestina* was tested by comparing the gut pigment content at the 17 water samples of the 9 sampling stations during day and night by the paired-sample *t* test. The same statistical test was applied to test the diel difference in gut clearance rate of *P. avirostris* at the 17 water samples of the 9 sampling stations during day and night.

3.4 Results

3.4.1 Physical parameters and chlorophyll concentration

The study was carried out in early summer when water temperature in Tolo Harbour was just beginning to increase. Vertical profiles of water temperature at the 9 stations are shown in Fig. 3.3.

Water temperature ranged from 23 to 27°C. Day and night water temperatures were very similar. A thermocline was present in the water column. Temperature was highest at the surface, decreased down the water column and remained almost constant below 4 or 6 m.

Level of dissolved oxygen ranged from 6.0 to 12.3 mg L^{-1} (Fig. 3.4) and the highest levels were recorded near the surface. At most stations, dissolved oxygen concentrations at the surface were higher in daytime than at night.

Salinity ranged from 35 to 38‰ (Fig. 3.5), suggesting that the water was more oceanic than estuarine. Salinity in the offshore stations was lower near the surface than in the deeper layers, indicating the presence of a halocline.

Secchi depth values taken during the day ranged from 1.3 to 2 m. Light intensity remained relatively constant throughout the day, with values ranging from 164.7 to 169.1 μE m^{-2} s^{-1}. Wind was blowing mostly from the northeast at speeds ranging from 0.8 to 4.7 m s^{-1}. Current driven by flood tide flowed towards the southwest along Tolo Channel during the day. Nighttime sampling was carried out during low tide when water flowed northeastward towards the entrance of the harbour.

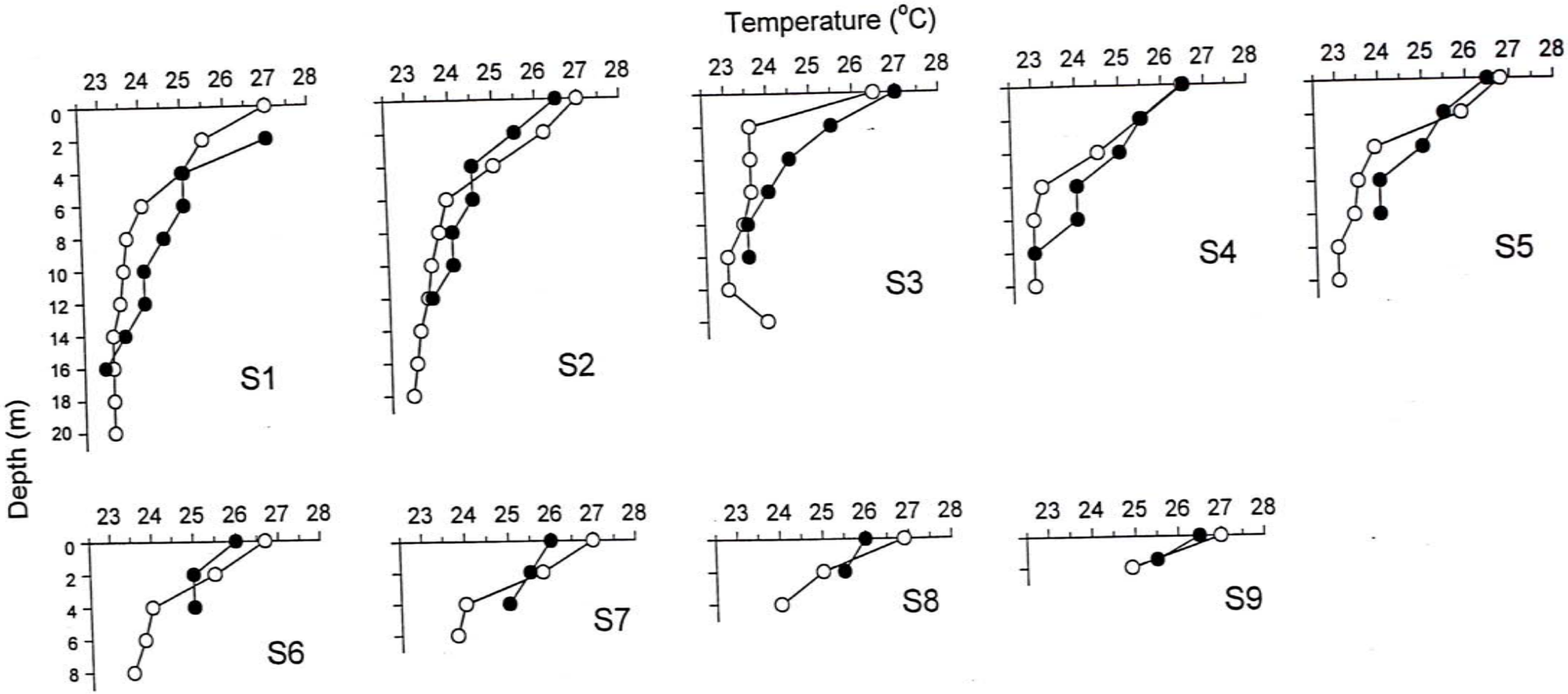


Fig.3.3 Vertical temperature profiles at 9 stations in Tolo Harbour on 23 May 1996. Open circles represent day and solid circles represent night.

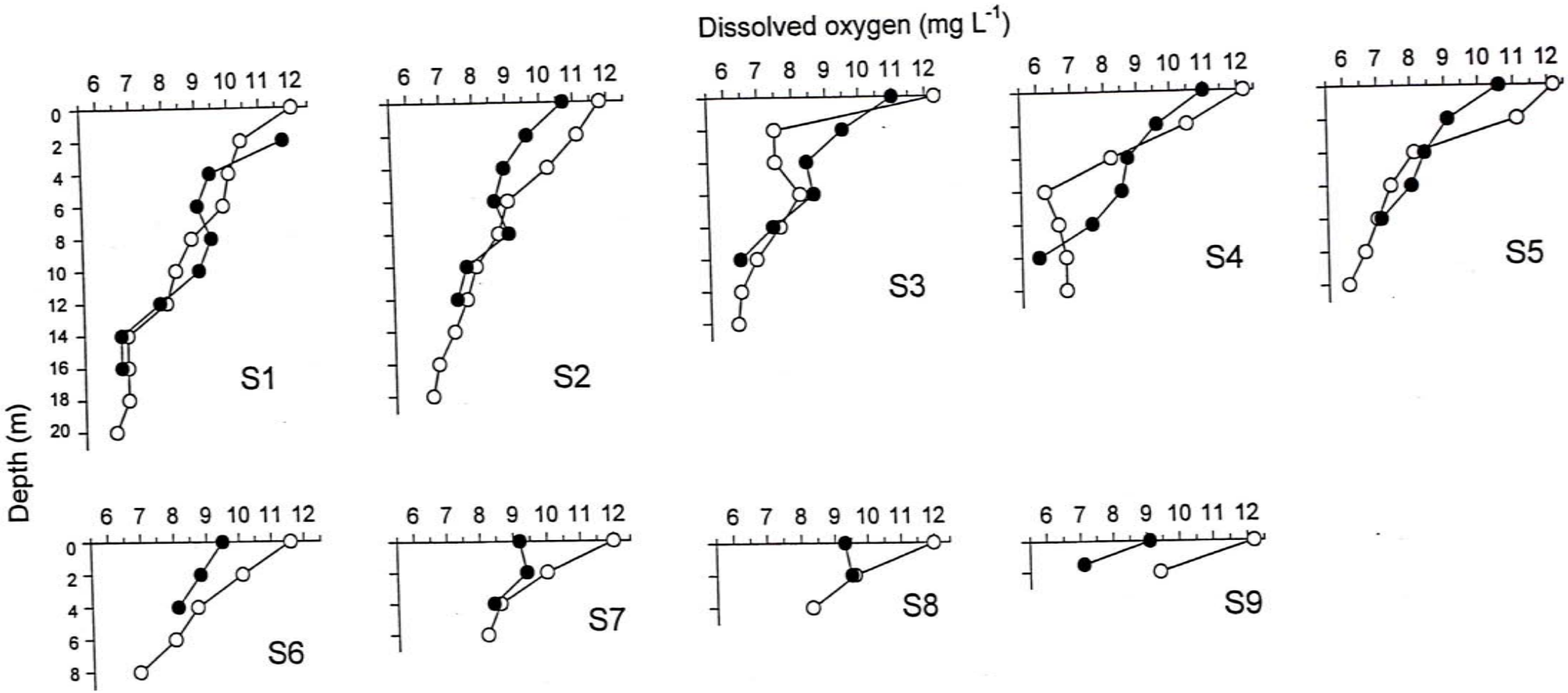


Fig.3.4 Vertical dissolved oxygen profiles at 9 stations in Tolo Harbour on 23 May 1996. Open circles represent day and solid circles represent night.

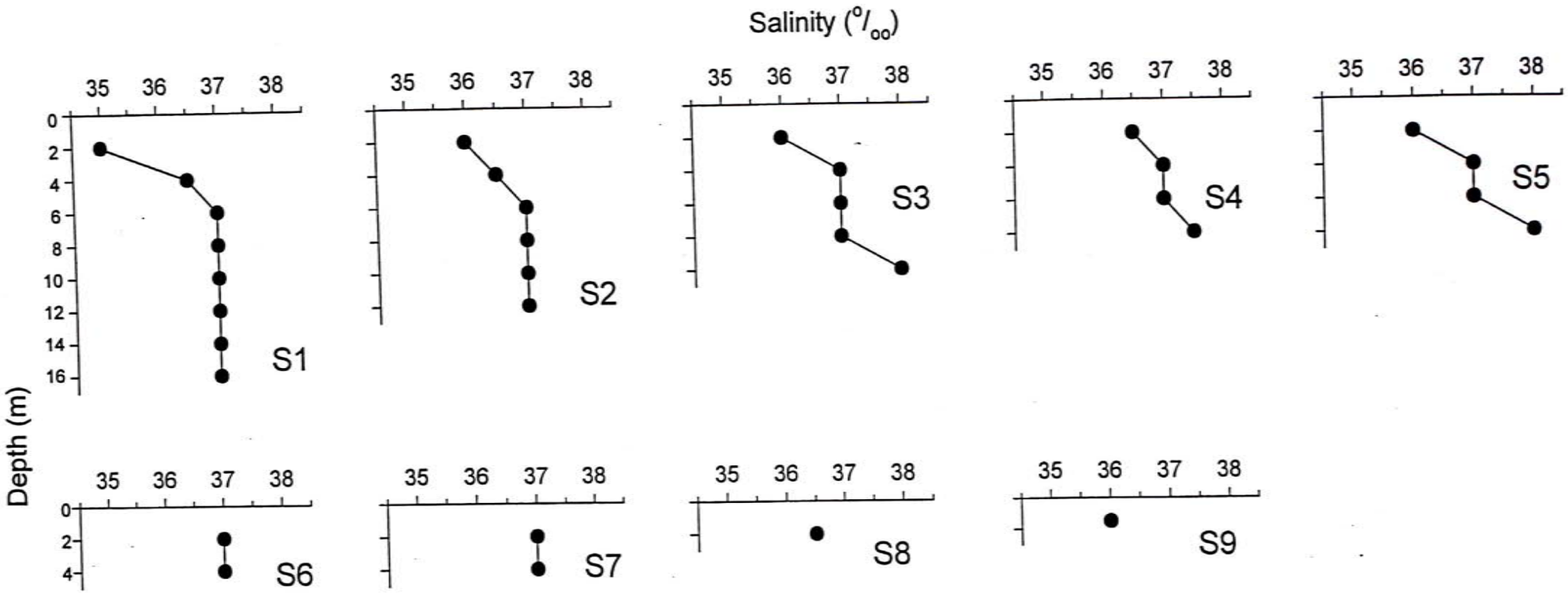


Fig.3.5 Vertical salinity profiles at 9 stations in Tolo Harbour on 23 May 1996. Values were taken at night.

Chlorophyll *a* concentration ranged from 6.24 and 17.59 ng mL^{-1}. The vertical profiles of chlorophyll *a* concentration at the 9 sampling stations are presented in Fig. 3.6. In general, values at the surface were higher in daytime than in nighttime. As expected, chlorophyll *a* concentrations were higher near the surface than in the lower parts of the water column.

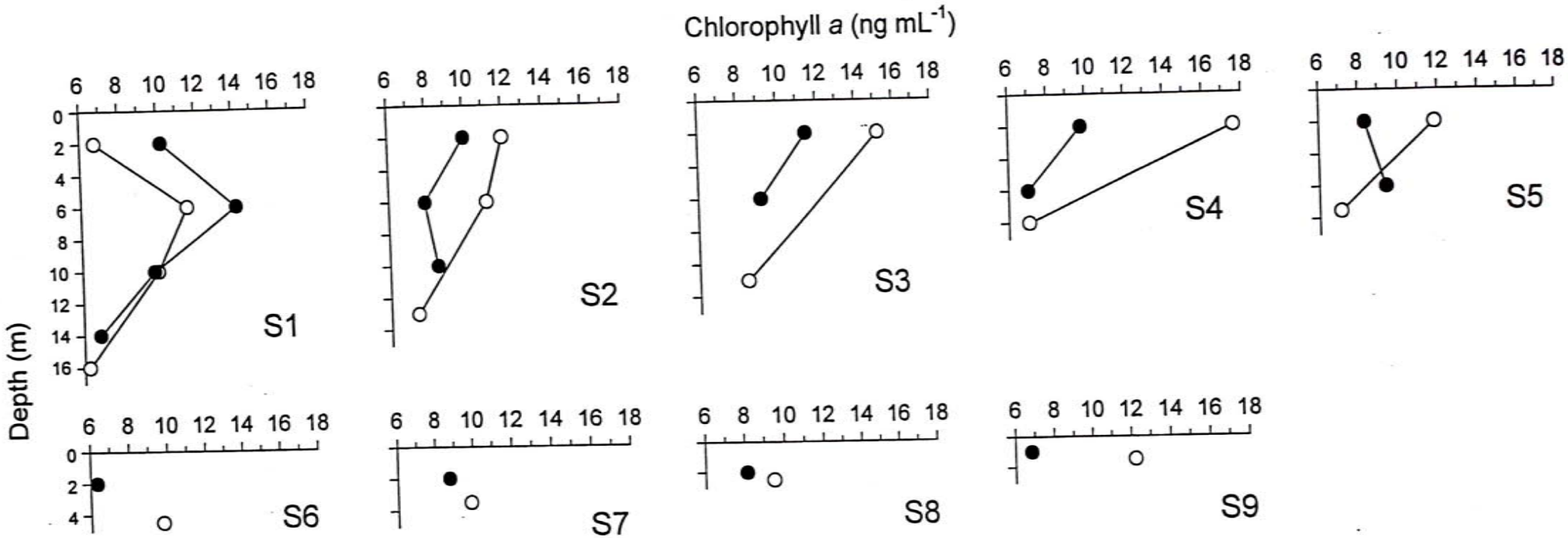


Fig.3.6 Vertical chlorophyll *a* profiles at 9 stations in Tolo Harbour on 23 May 1996. Open circles represent day and solid circles represent night.

3.4.2 Spatial and temporal distribution of marine cladocerans

3.4.2.1 Species composition and abundance

Samples collected from Tolo Harbour on 23 May 1996 contained 4 species of marine cladocerans: *Pseudevadne tergestina* (Plate 3.1), *Penilia avirostris* (Plate 3.2), *Podon* sp. (Plate 3.3A) and *Podon schmackeri* (Plate 3.3B). Overall average densities calculated from 9 sampling stations during day and night are listed in Table 3.1. *P. tergestina* constituted about 74% of the total marine cladoceran population during both day and night. A maximum density of 9920 ind. m^{-3} was recorded on the surface layer (0-4 m) of S5 during daytime (Fig. 3.7). The second most abundant species was *P. avirostris* which formed about 21% of the cladoceran population. *Podon* sp. and *P. schmackeri* occurred only in low numbers. Significant difference between day and night average densities was found for *Penilia avirostris* and *Pleopis schmackeri*, but not for *Pseudevadne tergestina* and *Podon* sp (Table 3.1).

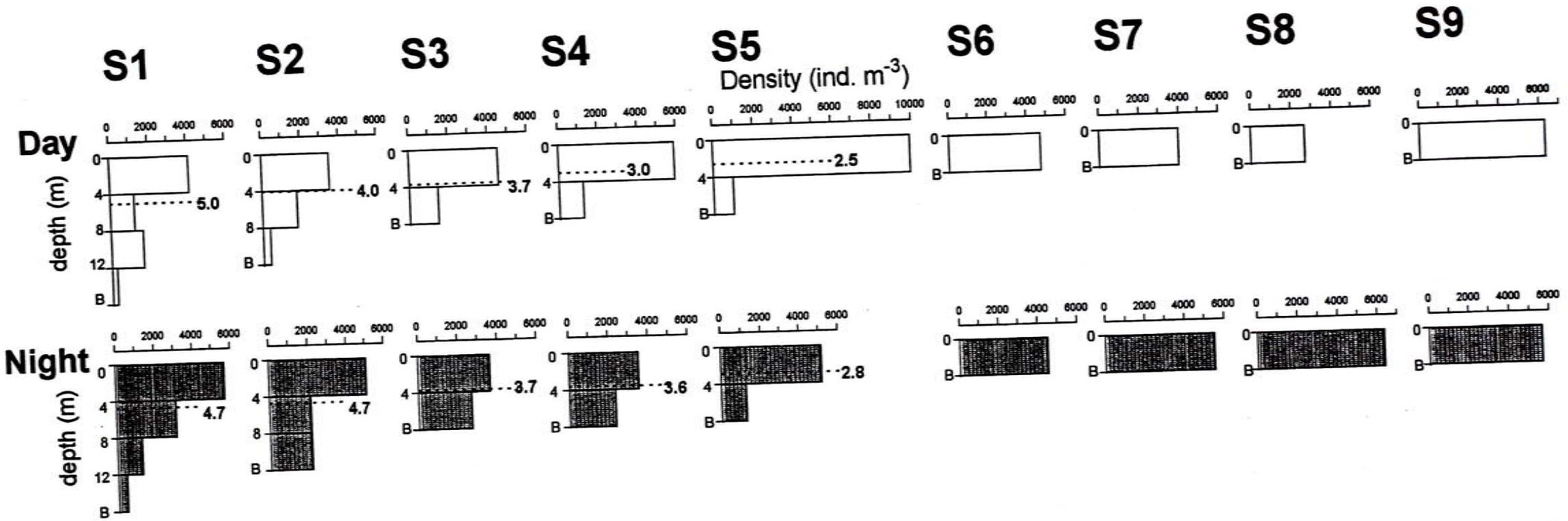


Fig.3.7 Vertical and horizontal distribution of *Pseudevadne tergestina* at 9 sampling stations in Tolo Harbour on 23 May 1996. Mean depths of the population at S1 to S5 are represented by broken lines. B represents the depth at 1 m above the bottom.

Table 3.1 Average density (ind. m^{-3}) of *Pseudevadne tergestina*, *Penilia avirostris*, *Podon* sp. and *Pleopis schmacker*i at 9 sampling stations in Tolo Harbour during day and night on 23 May 1996. Each average density presented here was calculated from the average densities of 9 sampling stations (n=9). Null hypothesis of no difference between average densities for day and night was tested by the paired-sample *t* test.

Species	**Day** (mean ± SE)	**Night** (mean ± SE)	**Difference**
Pseudevadne tergestina	3707 ± 518	4127 ± 471	ns (P=0.475)
Penilia avirostris	616 ± 65	1579 ± 205	s (P=0.005)
Podon sp.	352 ± 66	125 ± 45	ns (P=0.054)
Pleopis schmackeri	91 ± 26	17 ± 3	s (P=0.028)

s = significant difference, P<0.05
n.s. = no significant difference, P>0.05

3.4.2.2 Vertical and horizontal distribution in general population

Vertical and horizontal distribution of the 4 species of marine cladocerans in terms of density in 17 cross-sectional samples at 9 sampling stations in Tolo Harbour are illustrated in figures 3.7 to 3.10.

Vertical distribution

Reverse DVM was observed in *Pleopis schmackeri* (Fig. 3.10). The percentages of population in surface water (0-4 m) of the 5 offshore stations were significantly higher during daytime than during nighttime (P=0.007), although no significant difference in mean population depth was found between the day and night at the same 5 offshore stations. No diel vertical migration was observed in *Pseudevadne tergestina* (Fig. 3.7), *Penilia avirotris* (Fig. 3.8) and *Podon* sp. (Fig. 3.9).

Pseudevadne tergestina was an epiplankter. Most of the population stayed near the surface (0-4 m) during both day and night (Fig. 3.7).

Horizontal distribution

Diel horizontal migration was only exhibited by *Podon* sp. (Fig. 3.9). The percentages of population at the inshore stations were significantly higher during the day than during the night (P=0.005), indicating that individuals aggregated at the inshore regions during daytime and migrated to the offshore waters at night.

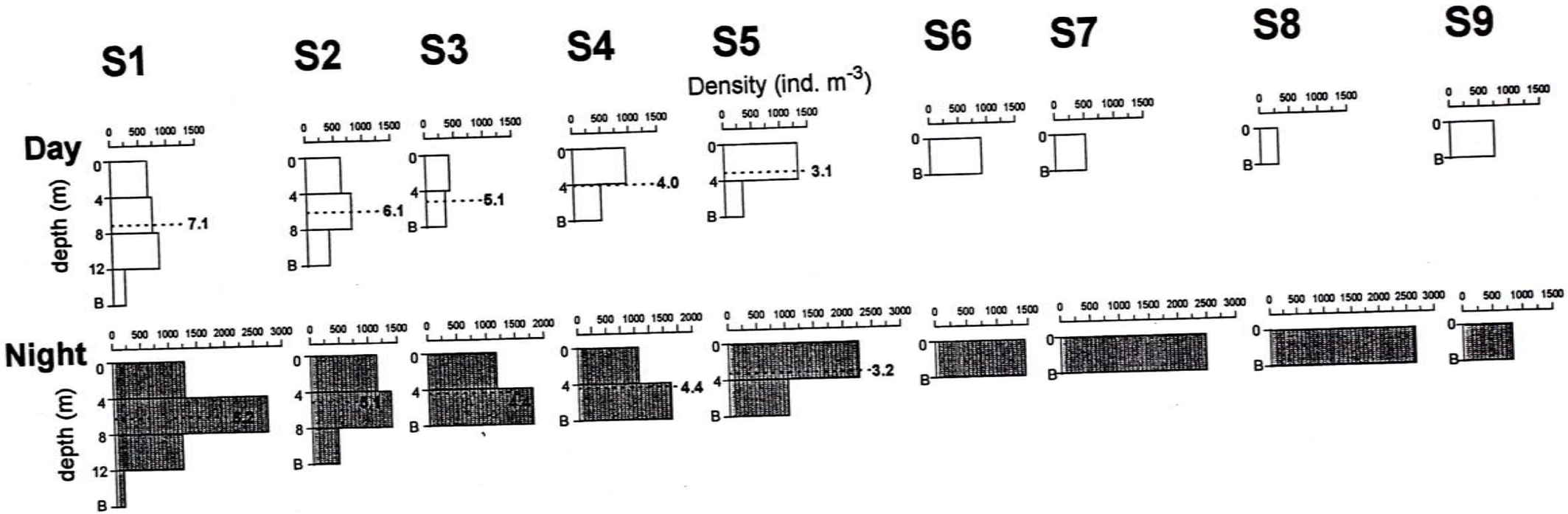


Fig.3.8 Vertical and horizontal distribution of *Penilia avirostris* at 9 sampling stations in Tolo Harbour on 23 May 1996. Mean depths of the population from S1 and S5 are represented by broken lines. B represents the depth at 1 m above the bottom.

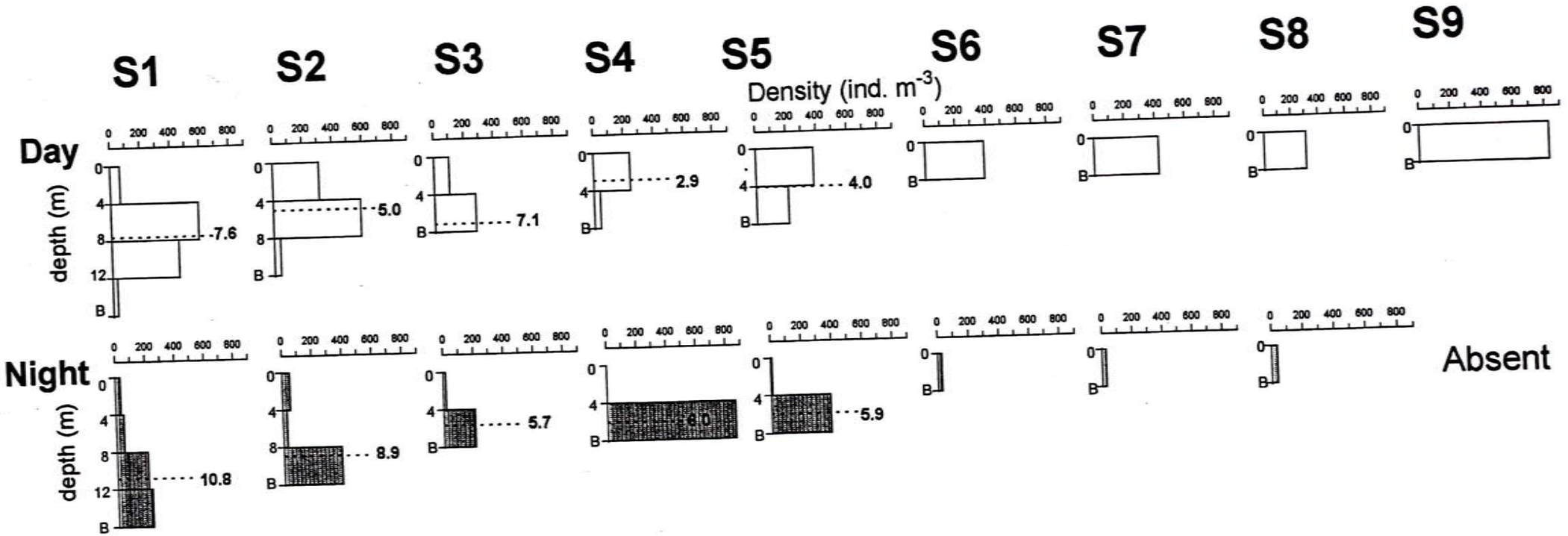


Fig.3.9 Vertical and horizontal distribution of *Podon* sp. at 9 sampling stations in Tolo Harbour on 23 May 1996. Mean depths of the population at S1 to S5 are represented by broken lines. B represents the depth at 1 m above the bottom.

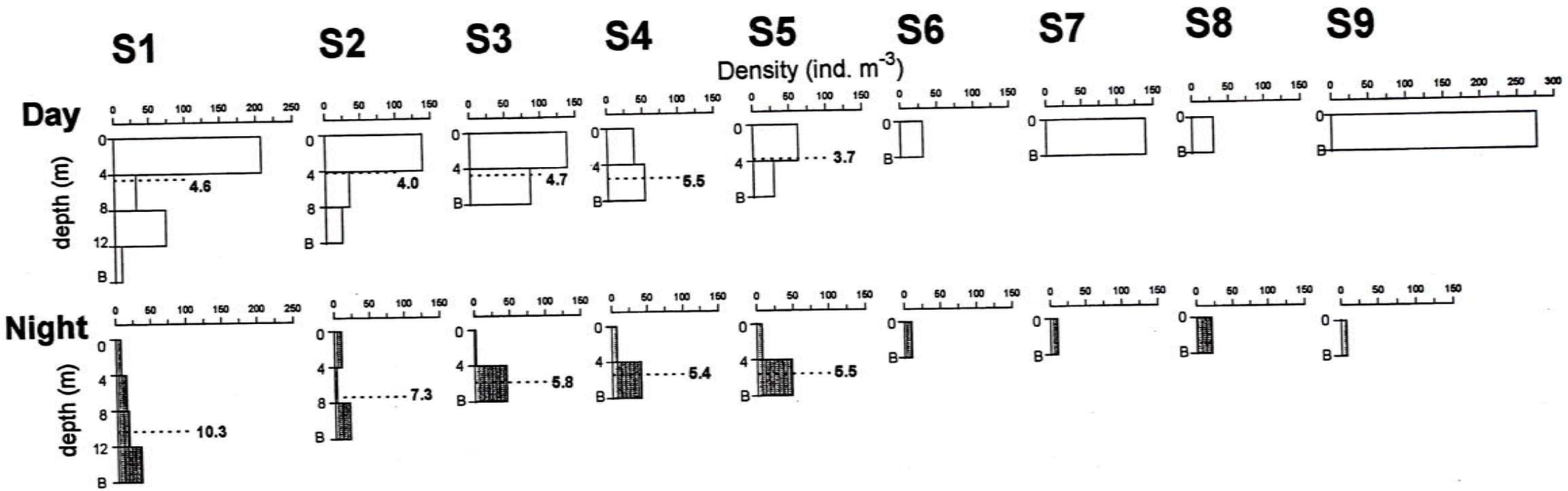


Fig.3.10 Vertical and horizontal distribution of *Pleopis schmackeri* at 9 sampling stations in Tolo Harbour on 23 May 1996. Mean depths of the population at S1 to S5 are represented by broken lines. B represents the depth at 1 m above the bottom.

No diel horizontal migration behaviour was detected in *Pseudevande tergestina* (Fig. 3.7), *Penilia avirostris* (Fig. 3.8) and *Pleopis schmackeri* (Fig. 3.10).

3.4.2.3 Vertical and horizontal patterns in size distribution

The body size distributions of *Pseudevadne tergestina*, *Penilia avirostris*, *Podon* sp. and *Pleopis schmackeri* collected in Tolo Harbour on 23 May 1996 are shown in Fig. 3.11. The body size range and mean body size of the four species during day and night are listed in Table 3.2. *P. tergestina* and *P. avirostris* were bigger than *Podon* sp and *P. schmackeri*.

The mean body size of *Pseudevade tergestina*, *Penilia avirostris* and *Podon* sp. at the 9 sampling stations did not differ significantly between day and night (Table 3.2). In comparison, the daytime population of *Pleopis schmackeri* was made up of significantly smaller individuals compared to the nighttime population.

The vertical and horizontal distributions of average body size of *Pseudevadne tergestina*, *Penilia avirostris*, *Podon* sp. and *Pleopis schmackeri* in 17 cross-sectional samples at 9 stations are shown in Fig. 3.12 to Fig. 3.15 respectively.

Vertical distribution

Pseudevadne tergestina (Fig. 3.12), *Penilia avirostris* (Fig. 3.13) and *Pleopis schmackeri* (Fig. 3.15) showed significant vertical variations in body size during daytime. The mean body size at the 5 offshore stations was significantly larger in the bottom (4 m to ~1 m above bottom) than in the surface water (0-4 m) for *P. tergestina* (P=0.026), *P. avirostris* (P=0.021) and *P. schmackeri* (P=0.0001) during daytime. However, vertical variations in body size were not observed at night. The disappearance of vertical variations in body size at night suggested that larger

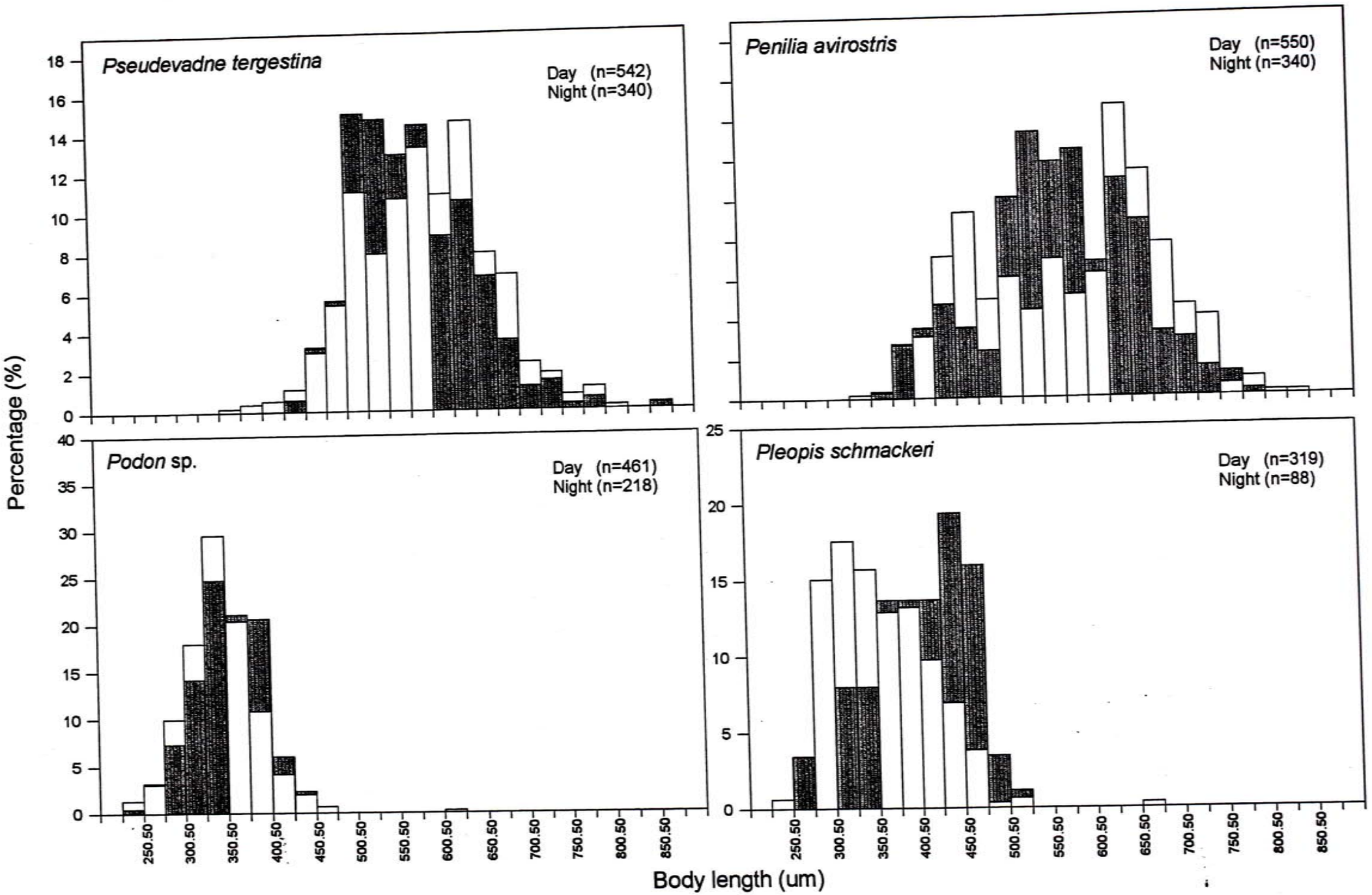


Fig.3.11 Size distribution of *Pseudevadne tergestina*, *Penilia avirostris*, *Podon* sp. and *Pleopis schmackeri*. Open bars = day, closed bar = night.

Table 3.2 Body size range and mean body size (μm) of *Pseudevadne tergestina*, *Penilia avirostris*, *Podon* sp. and *Pleopis schmackeri* collected at 9 sampling stations in Tolo Harbour during day and night on 23 May 1996. The mean sizes presented here represented the average from 9 sampling stations (n=9). The mean body size of *Podon* sp. was calculated from 8 sampling stations only (n=8) because this species was absent in S9 during nighttime. The null hypothesis of no difference between day and night average size was tested by paired-sample *t* test.

Species	**Size range**	**Day** (mean ± SE)	**Night** (mean ± SE)	**Difference**
Pseudevadne tergestina	356.2-852.1	584.1 ± 3.0	572.6 ± 4.7	ns (P=0.107)
Penilia avirostris	347.8-834.7	563.3 ± 12.5	574.3 ± 6.0	ns (P=0.549)
Podon sp.	234.8-608.7	342.1 ± 3.8	351.9 ± 2.3	ns (P=0.080)
Pleopis schmackeri	226.1-652.1	351.8 ± 6.0	381.3 ± 9.4	s (P=0.027)

s = significant difference, P<0.05
n.s. = no significant difference, P>0.05

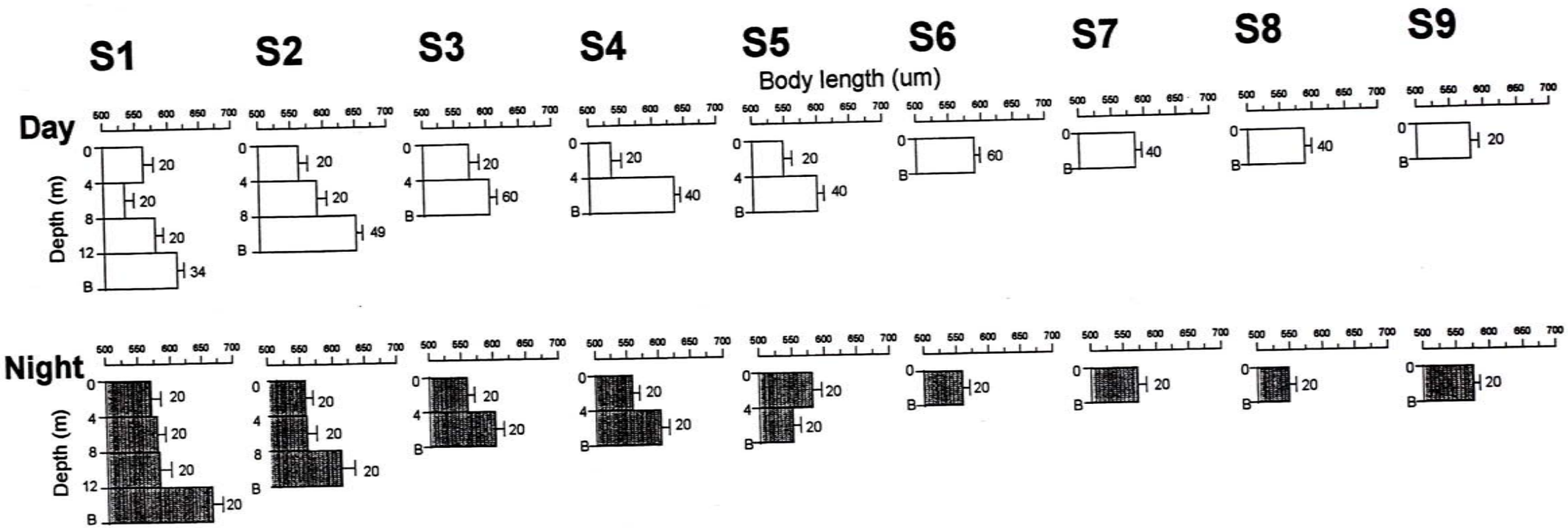


Fig.3.12 Body size distribution (mean ± SE) of *Pseudevadne tergestina* at 9 sampling stations in Tolo Harbour on 23 May 1996. Number beside each error bar represents the number of individuals measured in each sample. B represents the depth at 1 m above the bottom.

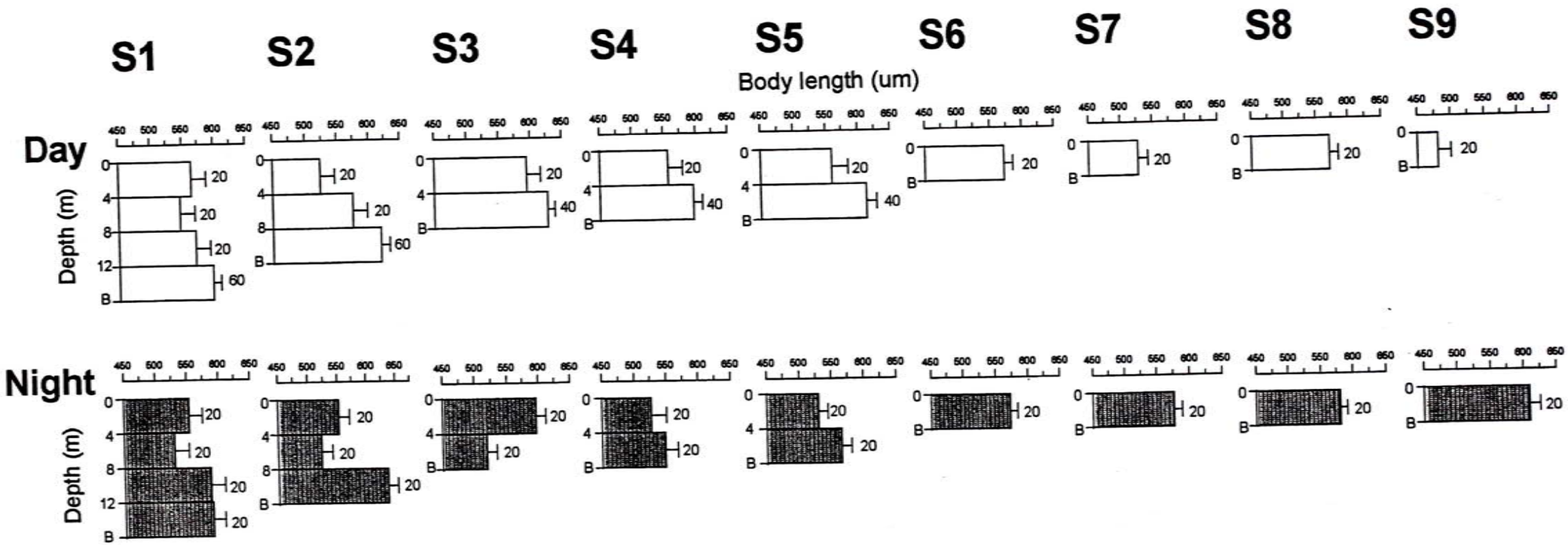


Fig.3.13 Body size distribution (mean ± SE) of *Penilia avirostris* at 9 sampling stations in Tolo Harbour on 23 May 1996. Number beside each error bar represents the number of individuals measured in each sample. B represents the depth at 1 m above the bottom.

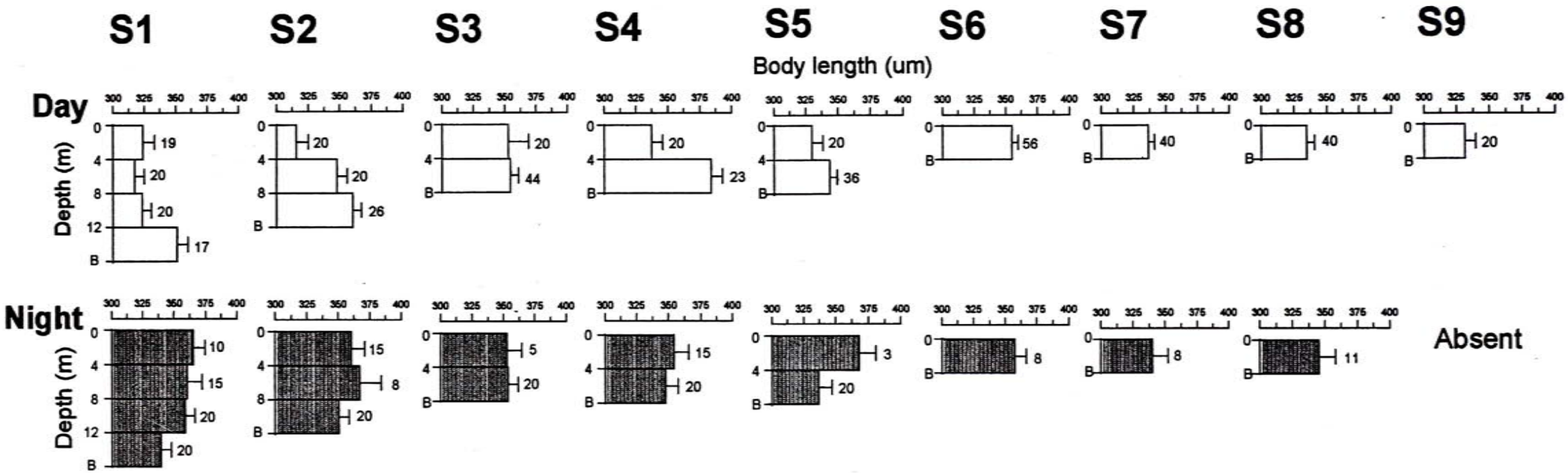


Fig.3.14 Body size distribution (mean ± SE) of *Podon* sp. at 9 sampling stations in Tolo Harbour on 23 May 1996. Number beside each error bar represents the number of individuals measured in each sample. B represents the depth at 1 m above the bottom.

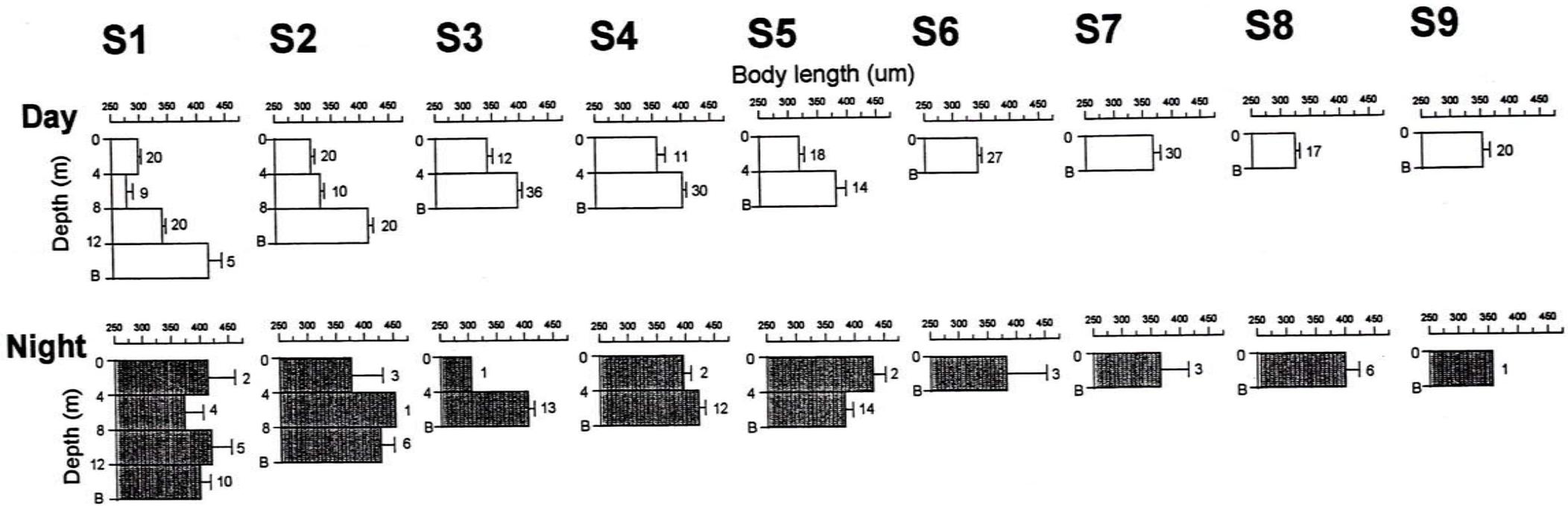


Fig.3.15 Body size distribution (mean ± SE) of *Pleopis schmackeri* at 9 sampling stations in Tolo Harbour on 23 May 1996. Number beside each error bar represents the number of individuals measured in each sample. B represents the depth at 1 m above the bottom.

individuals of *P. tergestina*, *P. avirostris* and *P. schmackeri* actively avoided the well-illuminated surface water during daytime and migrated upward to the surface at night.

No vertical variations in body size were observed in *Podon* sp. (Fig. 3.14) during both day and night.

Horizontal distribution

No horizontal variation in body size was observed in the 4 populations of *Pseudevadne tergestina* (Fig. 3.12), *Penilia avirostris* (Fig. 3.13), *Podon* sp. (Fig. 3.14) and *Pleopis schmackeri* (Fig. 3.15).

3.4.2.4 Distribution of marine cladocerans at different stages

Penilia avirostris

All individuals of *Penilia avirostris* collected were parthenogenetic females. No sexual individual was found in the samples. Non-gravid females included immature females and mature females which had released their broods (Cheng and Chen 1966). The vertical and horizontal distributions of *Penilia avirostris* females with large embryos, with small embryos and without embryo are presented in Fig. 3.16, Fig. 3.17 and Fig. 3.18 respectively. Parthenogenetic females without embryo formed the greatest part of the *P. avirostris* population during both day and night (Table 3.3). About 50% of the *Penilia* population consisted of non-gravid females and the densities did not differ significantly between day and night (Table 3.3). In contrast, the percentage of *P. avirostris* with large embryos was significantly higher at night than during the day, while the percentage of females bearing small embryos was significantly higher during the day than during the night (Table 3.3).

Vertical distribution of *Penilia avirostris* at 3 reproductive stages

The vertical and horizontal distributions of *Penilia avirostris* females with large embryos at 9 sampling stations are shown in Fig. 3.16. Although nocturnal upward migration was not detected when the entire population of *P. avirostris* was considered, it was clearly evident among females with large embryos. Mean depths of population at the 5 offshore stations (S1 to S5) were significantly deeper during daytime than during nighttime (P=0.008). In addition, the percentages of population in

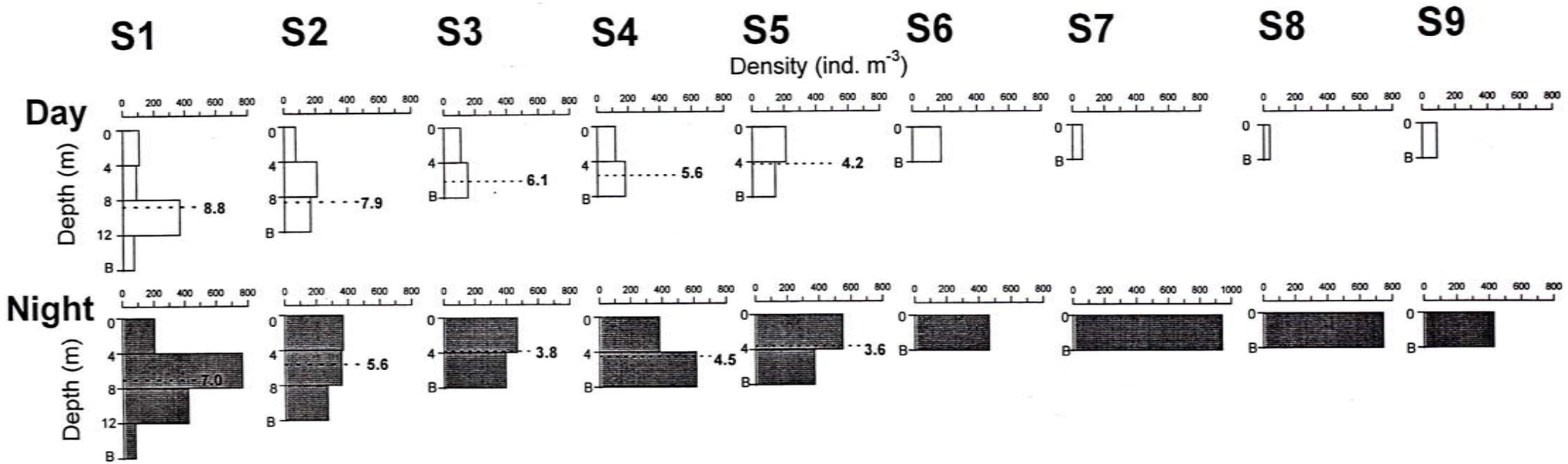


Fig. 3.16 Distribution of *Penilia avirostris* carrying large embryos (development stage III or above) at 9 sampling stations in Tolo Harbour on 23 May 1996. Mean depths of the population at S1 to S5 are represented by broken lines. B represents the depth at 1 m above the bottom.

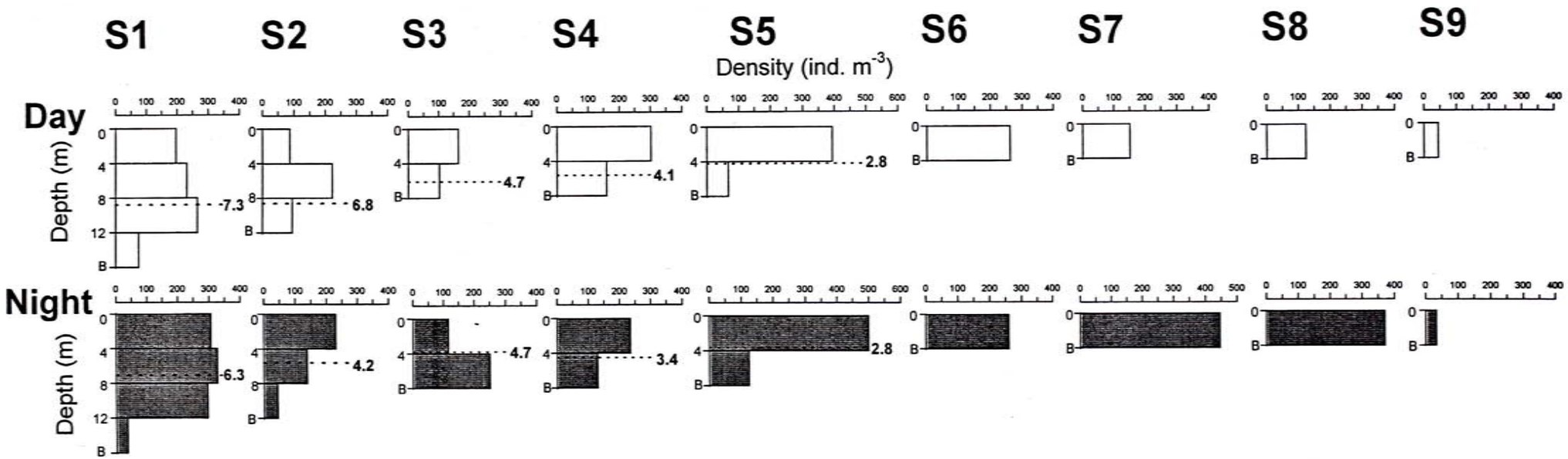


Fig. 3.17 Distribution of *Penilia avirostris* carrying small embryos (development stage I or II) at 9 sampling stations in Tolo Harbour on 23 May 1996. Mean depths of the population at S1 to S5 are represented by broken lines. B represents the depth at 1 m above the bottom.

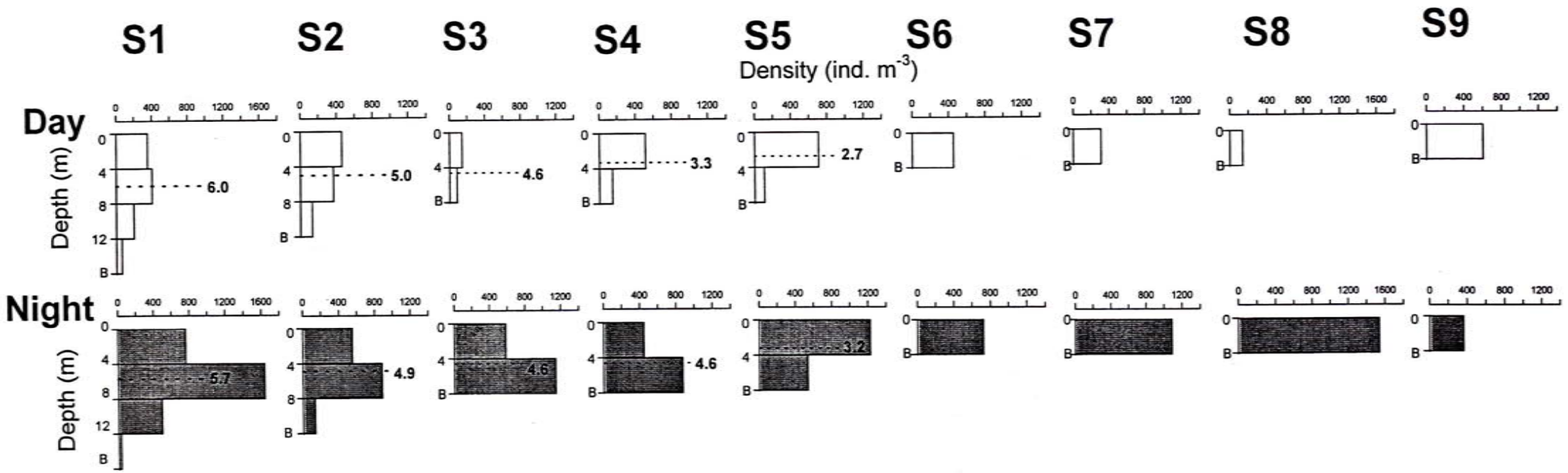


Fig. 3.18 Distribution of *Penilia avirostris* without embryo at 9 sampling stations in Tolo Harbour on 23 May 1996. Mean depths of the population at S1 to S5 are represented by broken lines. B represents the depth at 1 m above the bottom.

Table 3.3 Percentage (%) of parthenogenetic females of *Penilia avirostris* of different reproductive stages at 9 sampling stations in Tolo Harbour on 23 May 1996. Percentage presented here represented the average percentages of 9 sampling stations (n=9). The null hypothesis of no difference between day and night was tested by paired-sample *t* test using arsine transformed data.

Reproductive stage	**Day** (mean ± SE)	**Night** (mean ± SE)	**Difference**
With large embryos (parthenogenetic embryos at stage III or above)	22.3 ± 2.9	35.6 ± 2.4	s (P=0.017)
With small embryos (parthenogenetic embryos at stage I or II)	28.2 ± 3.3	14.8 ± 1.7	s (P=0.001)
Without embryo	49.5 ± 4.9	49.6 ± 1.8	ns (P=0.988)

s = significant difference, P<0.05
n.s. = no significant difference, P>0.05

surface water (0-4 m) of the 5 offshore stations were significantly higher during the night than during the day (P=0.047).

The vertical and horizontal distribution of *Penilia avirostris* females with small embryos and without embryo are shown in Fig. 3.17 and Fig. 3.18 respectively. Females at these two reproductive stages did not show evidence of DVM.

Horizontal distribution of *Penilia avirostris* at 3 reproductive stages

No diel horizontal migration was observed in *Penilia avirostris* females with large embryos, small embryos and without embryo.

Pseudevadne tergestina

Pseudevadne tergestina showed pronounced reproductive periodicity. Maturation of broods appeared to be triggered by darkness. Individuals contained parthenogenetic eyed-embryos only at night. The vertical and horizontal distribution of *P. tergestina* with eyed-embryos are shown in Fig. 3.19. Individuals carrying eyed-embryos were found mostly in surface water.

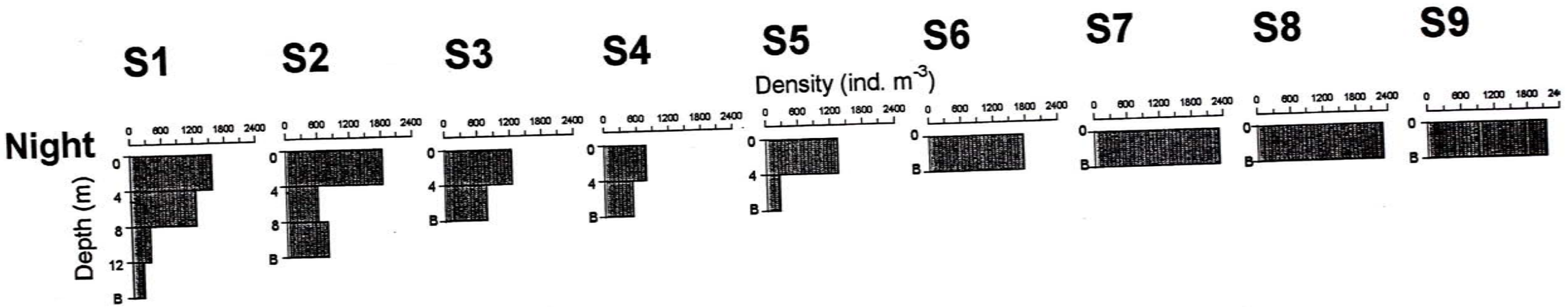


Fig.3.19 Vertical and horizontal distribution of *Pseudevadne tergestina* with eyed-embryo at 9 sampling stations in Tolo Harbour on 23 May 1996. Mean depths of the population at S1 and S2 are represented by broken lines. B represents the depth at 1 m above the bottom.

3.4.3 Feeding ecology of marine cladocerans

3.4.3.1 Diel variation in gut pigment content

Pronounced nocturnal increase (P=0.047, n=17) in gut pigment level was detected in *Penilia avirostris*. Gut pigment content averaged 0.40 ng ind.$^{-1}$ at night and 0.31 ng ind.$^{-1}$ during daytime. Fig. 3.20 shows that the pigment content of *P. avirostris* was not related to the change in ambient chlorophyll *a* concentrations.

Intense daytime feeding was observed in *Pseudevadne tergestina*. Gut pigment content was higher during the day than during the night (P=0.0002, n=17). Average values for day and night were 0.26 and 0.13 ng ind.$^{-1}$ respectively. As was in *Penilia avirostris*, the gut pigment difference was not due to change in chlorophyll *a* concentrations in the water column (Fig. 3.21).

Gut pigment content was not measured for *Podon* sp. and *Pleopis schmackeri* as the number of animals in some of the samples was too low for quantitative analysis.

3.4.3.2 Gut evacuation rate

Gut evacuation experiments were carried on 12 March 1997. Water temperature during the experimental bucket was about 20°C.

Gut evacuation of *Penilia avirostris* is shown in Fig. 3.22. Gut pigment level of *P. avirostris* declined rapidly when the animals were transferred into filtered seawater and reached relatively low levels after 10-15 minutes. Only gut pigment values during the first 30 minutes of gut evacuation were used to determine the

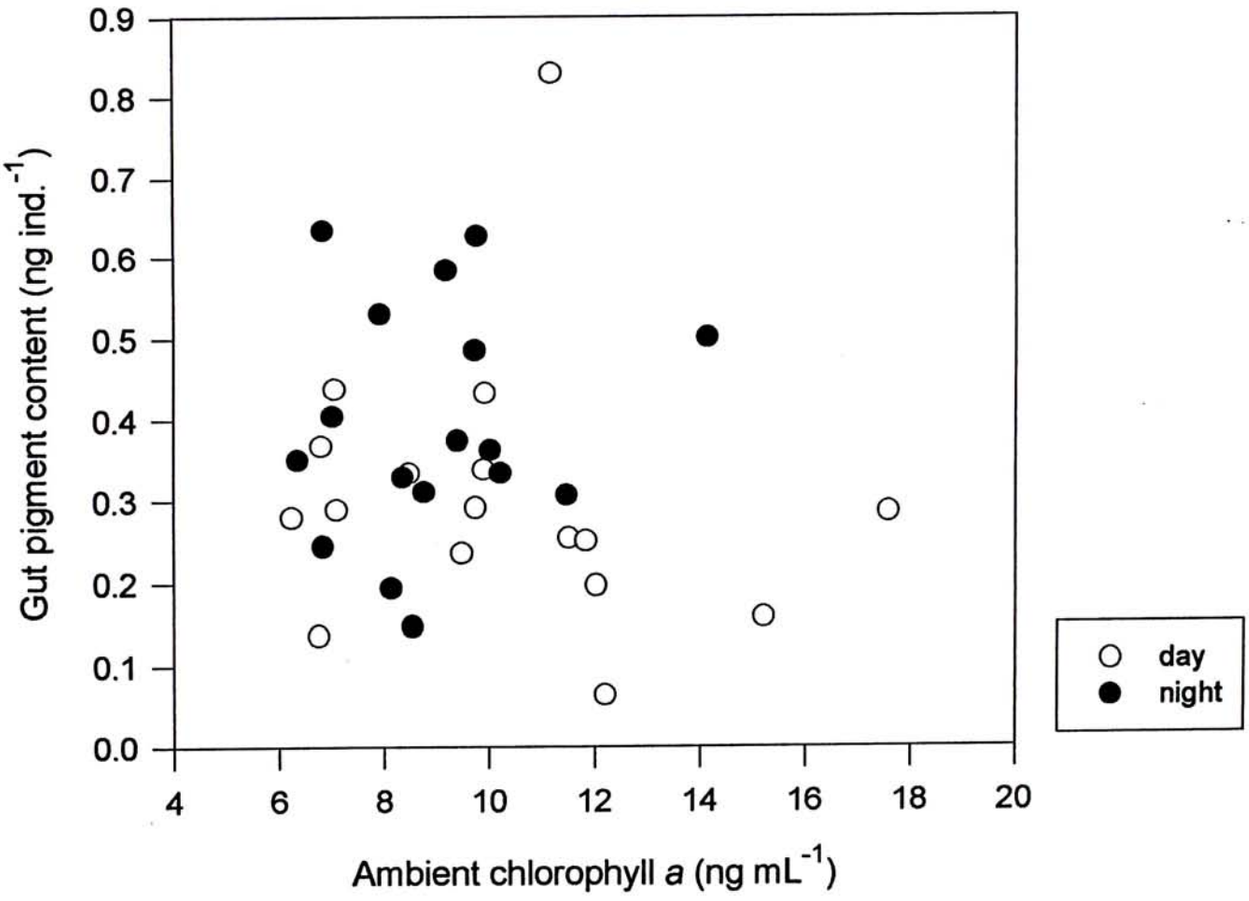


Fig. 3.20 Relationship between gut pigment content of *Penilia avirostris* and ambient chlorophyll *a* concentration in Tolo Harbour during day and night on 23 May 1996.

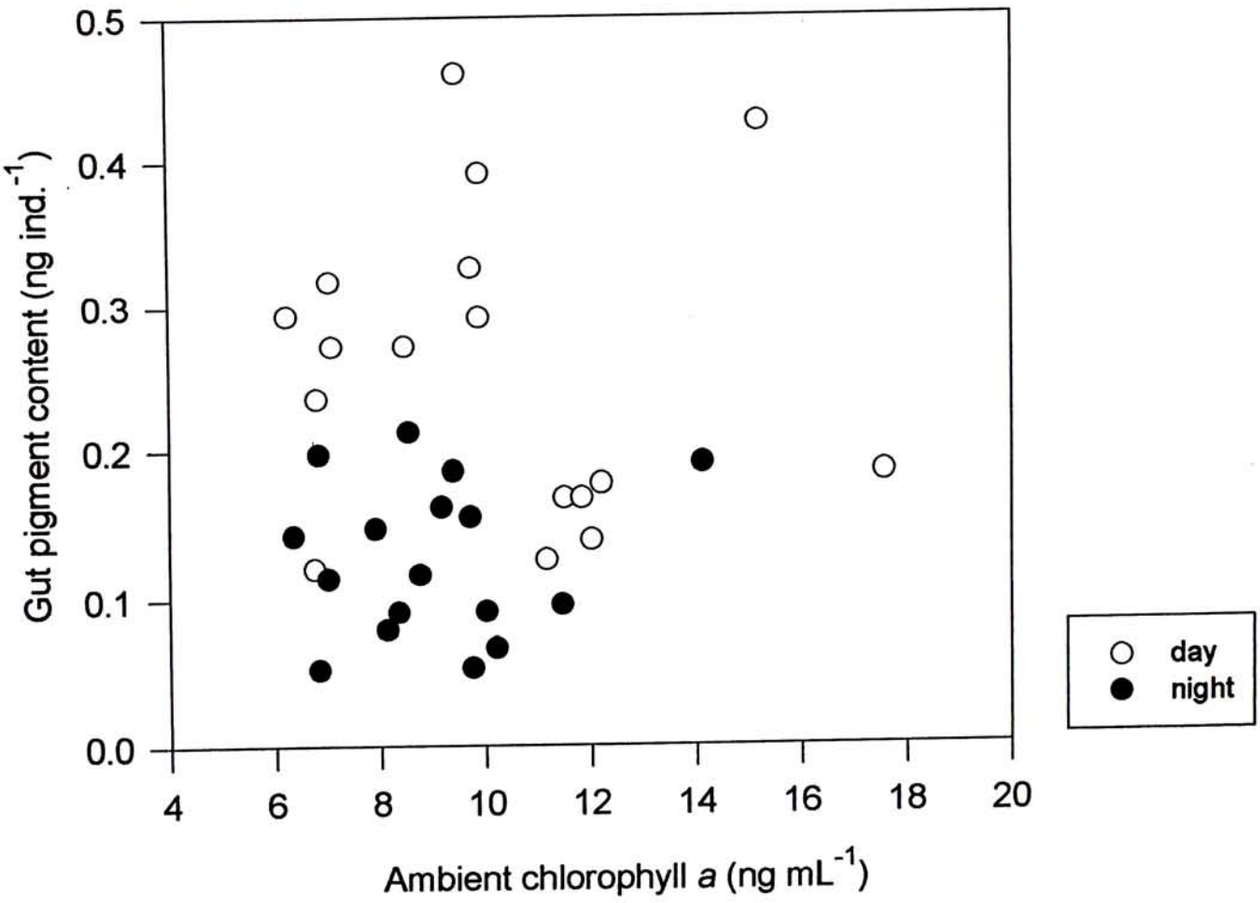


Fig. 3.21 Relationship between gut pigment content of *Pseudevadne tergestina* and ambient chlorophyll *a* concentration in Tolo Harbour during day and night on 23 May 1996.

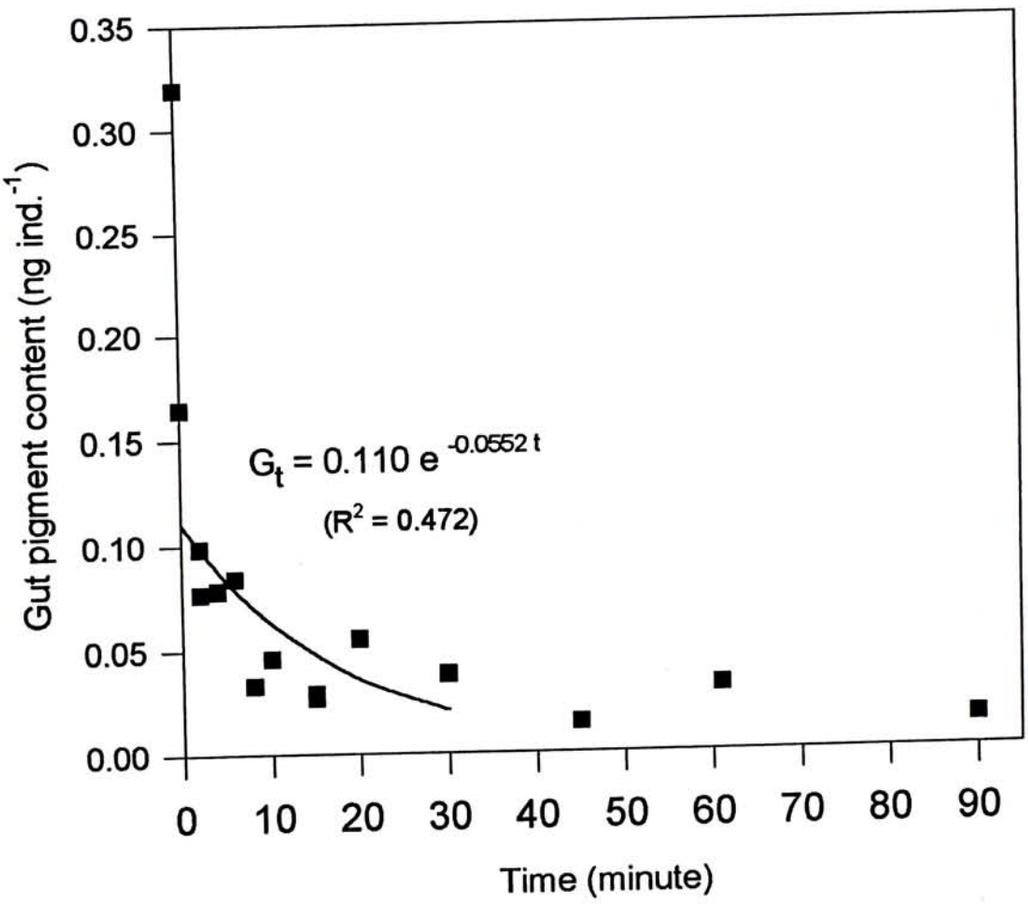


Fig. 3.22 Gut evacuation of *Penilia avirostris*

exponential equation. An evacuation rate constant (K) of 0.055 min^{-1} (R^2 = 0.472) was obtained.

Gut pigment levels of *Podon* sp. decreased gradually after the animals were transferred into filtered seawater (Fig. 3.23). All gut pigment values obtained during the 90-minute experiment were used to fit the exponential equation. The value of the evacuation rate constant (K) was 0.0211 min^{-1} (R^2 = 0.840).

The number of *Pseudevadne tergestina* and *Pleopis schmackeri* collected was too low for gut evacuation experiment.

3.4.3.3 Diel changes in clearance rate of *Penilia avirostris*

As data for both gut pigment content and gut evacuation rate were available only for *Penilia avirostris*, clearance rates could only be calculated for this species.

Clearance rates (Fig. 3.24) were significantly higher during the night than during the day (P=0.0243, n=17). Average values for day and night were 2.63 and 3.62 mL $ind.^{-1}$ day^{-1} respectively.

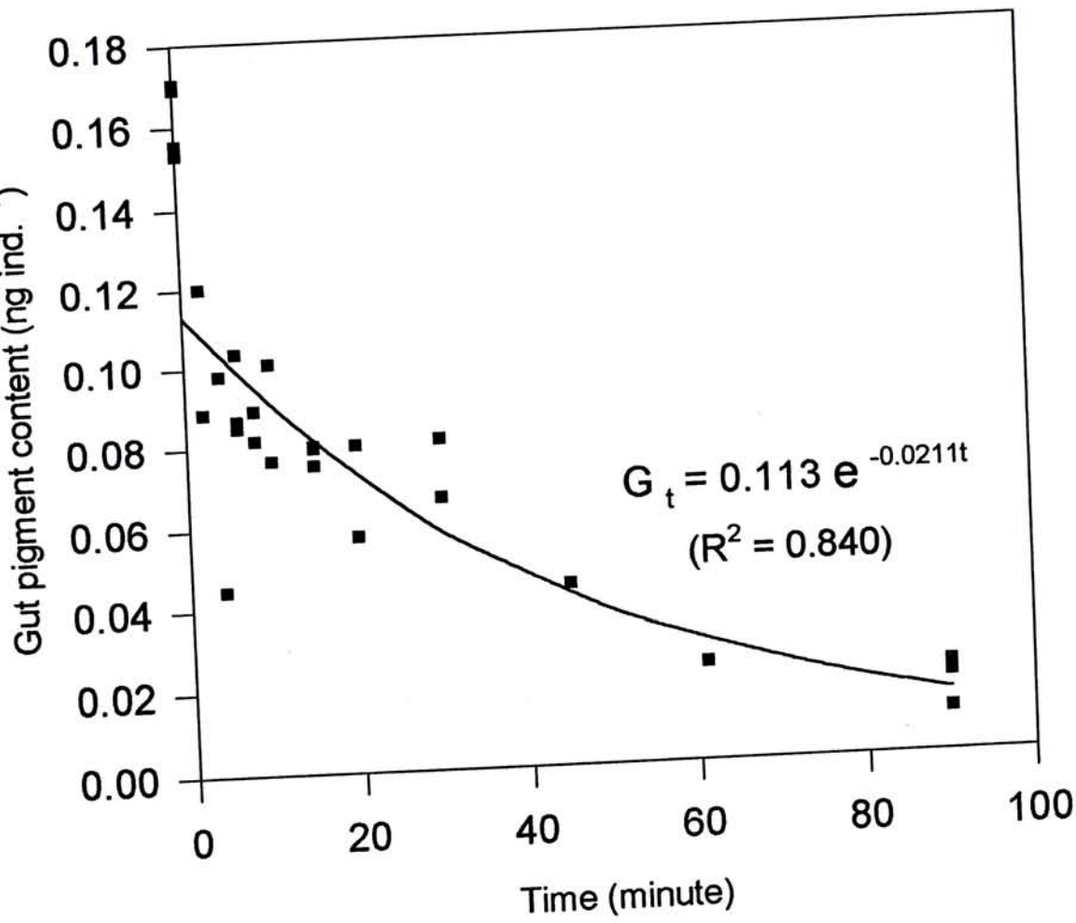


Fig. 3.23 Gut evacuation of *Podon* sp.

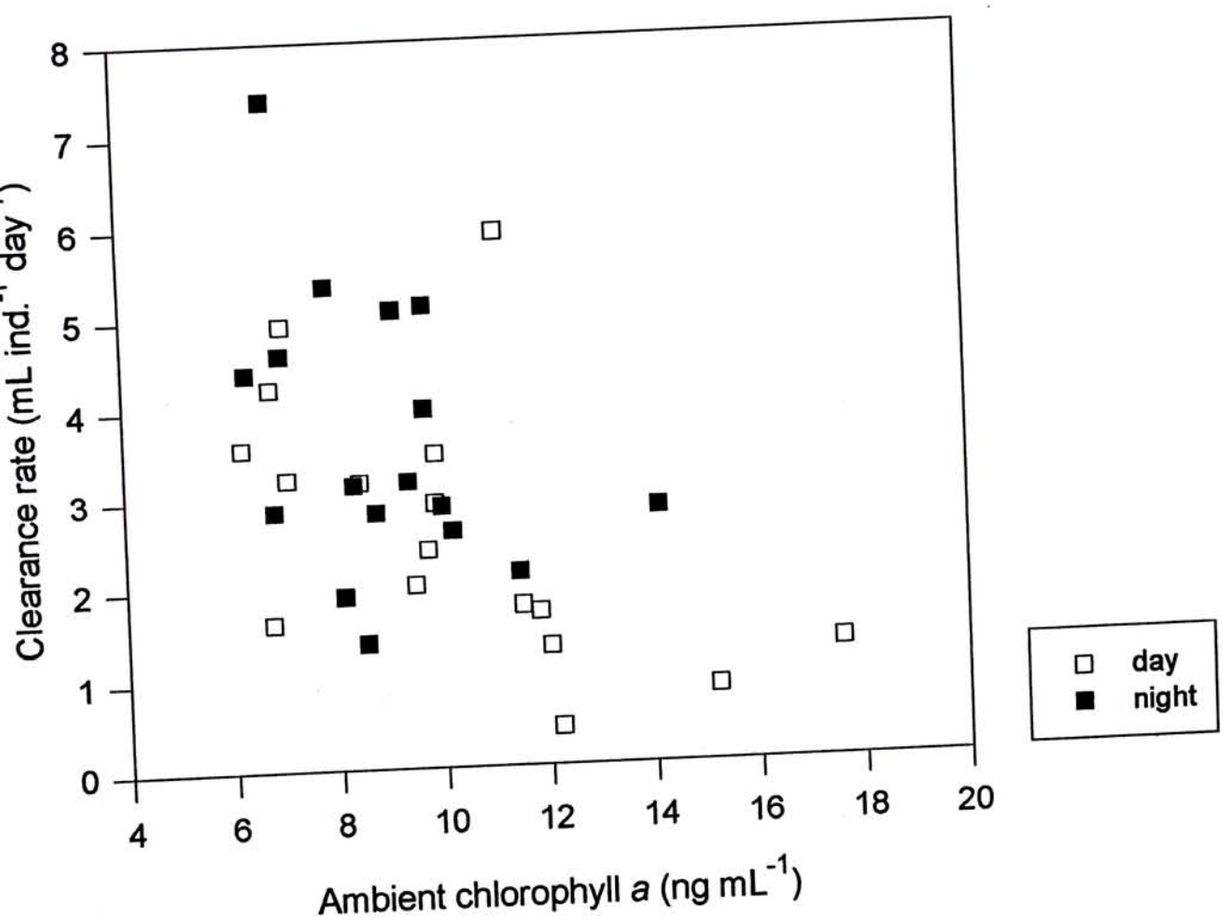


Fig. 3.24 Relationship between clearance rate of *Penilia avirostris* and ambient chlorophyll *a* concentration in Tolo Harbour during day and night on 23 May 1996.

3.5 Discussion

Four species of marine cladocerans (*Pseudevadne tergestina*, *Penilia avirostris*, *Podon* sp. and *Pleopis schmackeri*) were found in Tolo Harbour on 23 May 1996. In previous studies conducted in Tolo Harbour (Chen 1982; Chan 1991; Tang 1993), only *P. tergestina*, *P. avirostris* and *P. schmackeri* were identified. *Podon* sp. (Plate 3.3A) was probably overlooked by these previous investigators because of its morphological similarity to *P. schmackeri* (Plate 3.3B).

Pseudevadne tergestina was the most abundant cladoceran in Tolo Harbour on 23 May 1996. Average density among the 17 cross-sectional samples was often >3000 ind. m^{-3} and a maximum density of 9,920 ind. m^{-3} was recorded. While *P. tergestina* outnumbered *Penilia avirostris* in this study, a previous study by Tang *et al.* (1995) showed that *P. avirostris* was more abundant than *P. tergestina* during most parts of the year in Tolo Harbour and coastal waters in various parts of southern China.

Pleopis schmackeri occurred in low densities in this study. The overall *P. schmackeri* average density was about 50 ind. m^{-3}. Density of *P. schmackeri* in coastal waters around Japan (Onbé 1983) and the northwestern Pacific (Kim and Onbé 1989a) was also low. Much higher density of 150 ind. m^{-3} was reported by Tang *et al.* (1995) in Tolo Harbour during May 1991. However, it must be pointed out that the *P. schmackeri* counted by Tang *et al.* (1995) probably included both *Podon* sp. and *P. schmackeri.*

The body size of *Pseudevadne tergestina* and *Penilia avirostris* ranged from 356.2 to 852.1 μm and 347.8 to 834.7 μm respectively. The body length of *P. tergestina* was measured from the tip of the head to the dorso-posterior edge of the brood pouch. Individuals collected from Tolo Harbour in this study were somewhat

smaller than individuals collected in other regions. For example, size ranges of 640 to1300 μm has been reported from West Africa (Bryan 1979), 300 to 1000 μm from the Inland Sea of Japan (Onbé 1974) and 390 to 970 μm from Chesapeake Bay (Byran 1979). Similar observation was obtained for *P. avirostris*. Individuals collected from Tolo Harbour in this study were smaller than individuals from other areas. Maximum body size in Chinhae Bay of Korea (Yoo and Kim 1987), the Inland Sea of Japan (Onbé 1974) and coastal waters of China (Cheng and Chen 1966) were 1120, 950 and 1090 μm respectively. Moreover, the maximum body length recorded in the present study was shorter than that (1040 μm) recorded by Tang (1993) in the same area between 1990 and 1991, suggesting that the body size of individuals collected from a single location over a 24-hour period may not represent the actual size range of the species in Tolo Harbour.

Maturation of embryos in marine cladocerans is triggered by darkness (Mullin and Onbé 1992). In both *Pseudevadne tergestina* and *Penilia avirostris*, mature embryos were found in a higher percentage of females during the night than during the day. *P. tergestina* exhibited pronounced reproductive periodicity in the form of maturation of brood only at night. Embryos with well-developed pigmented eyes were found only at night. The absence of parthenogenetic females containing eyed-embryos during the day was probably caused by the release of all neonates near or before dawn (Bryan 1979; Mullin and Onbé 1992). In comparison, *P. avirostris*, which does not develop large compound eye, could carry large embryos at any time. Although the percentage of females with mature embryos was higher at night, the rhythmicity was not as rigid as that of *P. tergestina*. Similar observations had been reported from the Inland Sea of Japan and the Gulf of Mexico by Mullin and Onbé (1992).

Pseudevadne tergestina usually occupied shallower mean depths than the other three cladocerans during both day and night. Mullin and Onbé (1992) also reported that *P. tergestina* occurred in shallower water than *P. avirostris* in the Inland Sea of Japan. Similarly, *Podon* sp. usually occupied slightly deeper waters than *Pleopis schmackeri*.

Wind can strongly influence the horizontal distribution of zooplankton (Stavn 1971; George and Edwards 1976). Bast and Seitz (1993) suggested that the disturbing influence of wind and current can be minimized if samples were taken transversely to the direction of wind. In this study, the effects of wind and current on the samples were minimized because the sampling transect was set nearly perpendicular to the direction of wind and current.

In some cases, marine cladocerans in Tolo Harbour showed day-and-night difference in vertical and horizontal distribution. Diel difference in spatial distribution probably cannot be accounted for by the diel change in temperature, dissolved oxygen and chlorophyll *a* as these parameters changed only slightly between day and night during the study.

3.5.1 Diel vertical and horizontal distribution of 3 marine podonids: *Pseudevadne tergestina*, *Podon* sp. and *Pleopis schmackeri*

Pseudevadne tergestina was an epiplankter because most of the population was found in the surface layer (0-4 m) during both day and night. The surface-dwelling characteristic of *P. tergestina* has been reported in other marine environments such as the Inland Sea of Japan, the Gulf of Mexico (Mullin and Onbé 1992) and the eastern Pacific (Longhurst and Seibert 1972).

No vertical migration was observed in *Pseudevande tergestina* in Tolo Harbour, although reverse DVM by this species has been reported from seas around Japan and reverse migration was considered to be common among marine podonids (Onbé 1977; Mullin and Onbé 1992; Onbé and Ikeda 1995). On the other hand, *Pleopis schmackeri* exhibited pronounced reverse DVM. Although the migration patterns between the *P. tergestina* and *P. schmackeri* were different, both species preferred the well-illuminated surface water during daytime. Marine podonids with large compound eyes and powerful grasping mouthparts are generally considered to be predatory (Bainbridge 1958; Gieskes 1971b; Mordukhai-Boltovskoi 1968; Schram 1986; Cheng and Cao 1987; Jagger *et al.* 1988). Therefore, it is reasonable to assume that *P. tergestina* and *P. schmackeri* preferred to stay in the surface layer where light was available for visual predation.

Reverse migration may also serve as a mechanism to avoid predation by non-visual tactile feeding invertebrate predators which undergo normal DVM (Cooper 1983; Ohman *et al.* 1983; Levy 1990; Neill 1990; Frost and Bollens 1992; Herwig and Schindler 1996). Because invertebrate predators such as chaetonagths and comb jellies are common in Tolo Harbour, it can be speculated that downward migration by

Pleopis schmackeri at night is an adaptation to avoid the non-visual invertebrate predators. However, the reason for the non-migration of *Pseudevadne tergestina* and *Podon* sp. are still unclear.

Pseudevadne tergestina, *Podon* sp. and *Pleopis schmackeri* increased their predation risk by staying in the surface layer during the day in Tolo Harbour where the density of small planktivorous fish was high. Their large compound eyes also increased the visibility of podonids to planktivorous fish. *P. tergestina* seemed to act against visual predation by developing eyed-embryos only at night. Not a single female was found to carry eye-embryos during the day. Maturation of embryos (development of eyed-embryos) at night was probably a defense mechanism against visual predation (Bryan 1979). The pigmented eye is the most visible part of many planktonic animals. Zaret (1972) found in freshwater cladocerans that susceptibility to predation by planktivorous fishes was increased in individuals with a larger eye or with additional eyespots.

Podon sp. exhibited diel horizontal migration by moving from inshore to offshore at night. This podonid which probably feed visually might aggregate at inshore areas which were more illuminated than the offshore areas during daytime. At night, they retrieved from inshore areas and migrated to deeper waters in the offshore regions. Some freshwater cladocerans aggregated in the vegetated littoral zone during daytime to avoid predation by pelagic fish predators (Davies 1985; DeMeester *et al.* 1993; Kvam and Kleiven 1995). However, this predator avoidance hypothesis can be ruled out for podonids in this study because the inshore regions of Tolo Harbour contain no macrophytes.

In summary, *Pseudevadne tergestina*, *Podon* sp. and *P. schmackeri* preferred staying in the well-illuminated surface and inshore regions during daytime. This

phototatic response provided supportive evidence for the proposed visual predatory feeding habit among marine podonids.

3.5.2 Diel vertical and horizontal distribution of *Peilinia avirostris*

DVM was not observed in the whole population of *Penilia avirostris* in Tolo Harbour. Similar result was also reported in seas around Japan (Onbé 1997; Onbé and Ikeda 1995). However, previous studies carried out in different parts of the world revealed that *P. avirostris* may exhibit other migratory patterns ranging from normal DVM (Wong *et al.* 1992b) to reverse DVM (Pagano *et al.* 1993). The high degree of behavioural flexibility may be related to variations in the type (Frost and Bollens 1992) and intensity of predation pressure (Dini and Carpenter 1991) in various water bodies. Frost and Bollens (1992) observed that the migration behaviour of the copepod *Pseudocalanus newmani* was highly variable and included all 3 migratory patterns mentioned above. These authors suggested that reverse DVM, the most common migration mode in *P. newmani* at Dabob Bay, was induced by the presence of invertebrate predators which migrated normally. On the other hand, normal DVM by *P. newmani* suggested an occassional inducing role by visual predators such as zooplanktivorous fish.

Visual predators tended to select prey with the greatest conspicuousness (Lampert 1993). Fishes prefer the egg-carrying cladocerans to nonovigerous individuals of the same species (Bollens and Frost 1991; Flinkman *et al.* 1992; Brancelj and Blejec 1994), as the visibility of an individual is greatly enhanced by the presence of eggs. Flinkman *et al.* (1992) reported that egg-carrying females of *Podon* and *Bosmina* were preyed upon at a higher rate than the nonovigerous females by Baltic herrings in the northern Baltic Sea and the Gulf of Bothnia. Ovigerous *Podon intermedius* females were common in the stomachs of Baltic herrings even though they were relatively rare in the plankton samples (Flinkman *et al.* 1992). Similarly,

the main target group of *Daphnia hyalina* for fish predators were adult females with eggs (Brancelj and Blejec 1994).

Among *Penilia avirostris*, females carrying large embryos were the most conspicuous and, as a result they were expected to be the most vulnerable to visual predators. On the other hand, females with no embryos were the least conspicuous and would be the least vulnerable to visual predators. *P. avirostris* females with small embryos was probably exposed to predation pressure intermediate between the two extreme groups. *P. avirostris* with large embryos, small embryos and no embyro occupied different mean depths at the 5 offshore stations, S1 to S5. During the day, females with large embryos had the deepest mean depth, followed by females with small embryos. Females without embryo stayed nearest to the surface. It can be concluded that individuals that were more conspicuous would tend to stay in deeper water. This result is in agreement with what has been commonly observed for planktonic species (Raymont 1983). Brancelj and Blejec (1994) also provided supportive evidence for the above statement. They found that ovigerous females of *Daphnia* are situated in layers with <1% of day-light intensity during the day as a defense mechanism against visual predators.

Only *Penilia avirostris* females bearing large embryos exhibited normal DVM. In contrast, no DVM was observed in females bearing small embryos and non-gravid females. Similar findings have been reported in some freshwater cladocerans. Egg-bearing claodcerans often show normal DVM of greater amplitudes than nonovigerous individuals (Lampert 1993; Brancelj and Blejec 1994).

3.5.3 Size distribution of marine cladocerans

Three species of marine cladocerans: *Pseudevadne tergestina*, *Penilia avirostris* and *Pleopis schmackeri* exhibited similar patterns of vertical distribution in body size during the day. Individuals found in the deeper parts of the water column were larger than those found in the surface water during daytime.

Vertical size variation is a common phenomenon in freshwater cladocerans. Smaller individuals tended to stay nearer to the surface than larger individuals (Wagner and Seitz 1992; Watt and Young 1992; DeMeester *et al.* 1995). Avoidance of visual predators is generally assumed to be the underlying reason for larger individuals to avoid the well-illuminated surface during daytime (Wagner and Seitz 1992; Watt and Young 1992; DeMeester *et al.* 1995).

Visual predators tend to select prey which are larger and more conspicuous (Brooks and Dodson 1965; Flinkman *et al.* 1992; Lampert 1993). As a result, larger individuals are exposed to higher predation risk when compared to the smaller individuals. This differential predation pressure is particularly powerful in the surface where light is abundant. To avoid predation, larger individuals of the *Pseudevadne tergestina*, *Penilia avirostris* and *Pleopis schmackeri* tended to reside in the darker and deeper water during daytime. At night, the larger individuals of the 3 species migrated upward to exploit the food and gain demographic advantage in warmer surface waters (Kerfoot 1985; Dawidowicz and Loose 1992; Williamson *et al.* 1996). Upward migration could also be the result of natural dispersal as predation pressure at the surface began to ease at night (DeMeester *et al.* 1993). Dispersion of larger individuals from deeper water to the surface led to the absence of vertical variation in

body size of *Pseudevadne tergestina*, *Penilia avirostris* and *Pleopis schmackeri* along the water column.

A similar finding of vertical variations in body size distribution was reported by Mullin and Onbé (1992) for *P. tergestina* in a thermally stratified station in the Gulf of Mexico. The larger individuals were found slightly deeper in the water column than the smaller individuals during the day and also during the night.

3.5.4 Feeding behaviour of marine cladocerans

Gut pigment content and clearance rate of *Penilia avirostris* were significantly higher during the night than during the day. Nighttime feeding was observed in *P. avirostris* even no normal DVM was recorded in the whole population. This observation is another counter argument to Gauld (1953) who suggested that nocturnal feeding was simply the result of DVM as the animals move in and out of the food-rich surface layer in a food stratified water body.

Food seemed to be abundant throughout the water column in Tolo Harbour during the period of investigation. Chlorophyll *a* concentration in the 17 cross-sectional samples ranged from 6.24 to 17.59 ng mL^{-1}, suggesting that *Penilia avirostris* was probably not limited by the food availability in Tolo Harbour. *P. avirostris* did not fed continuously even though food was unlimited in the entire water column in Tolo Harbour. This finding is in contrast to suggestions that zooplankton feeds continuously whenever sufficient food is available (Gauld 1953; Hart 1977; Dagg and Grill 1980), but is in agreement with studies which show that feeding rhythm is exhibited by zooplankton even in homogenous food condition (Dawidowicz and Loose 1992; Dam and Peterson 1993) and high food concentrations (Makino *et al.* 1996).

Feeding rhythms of *Penilia avirostris* appeared to be related to the light-dark cycle (Makino *et al.* 1996). High light intensity may inhibit the feeding of zooplankton (Head *et al.* 1985; Stearn 1986). Nocturnal feeding by *P. avirostris* probably served as a mechanism to avoid visual predation because the conspicuousness of an individual was increased by its foraging movement and gut pigments (Dagg *et al.* 1989; Mourelatos *et al.* 1989).

As food concentration was high even in the bottom and there was no advantage for *Penilia avirostris* with large embryos and larger individuals of *Pseudevadne tergestina*, *P. avirostris* and *Pleopis schmackeri* to move into the surface water, why did these populations still migrated upward at night? Demographic advantages gained by staying in warmer water in the surface (Kerfoot 1985; Dawidowicz and Loose 1992; Williamson *et al.* 1996) may be the cause for the nocturnal ascent. Many species show higher growth rate and egg production rate in higher temperature (McLaren 1963a; Orcutt and Porter 1983). Dawidowicz and Loose (1992) showed that *Daphnia magna*, although in a homogenous food condition, migrated across the thermocline to the upper warmer water at night to avoid the disadvantage of staying permanently in colder water in the lower water column. A more striking example to demonstrate the uncoupling of feeding and DVM is that *Daphnia* and *Diaptomus* in Lake Waynewood migrated from the food-rich lower water column to the food-poor epilimnion during the night to benefit from the demographic advantage (Williamson *et al.* 1996). The purpose of leaving the oxygen-poor bottom layers could be another reason for upward migration of *P. avirostris* with large embryos and larger individuals of *Pseudevadne tergestina*, *P. avirostris* and *Pleopis schmackeri* (Hanazato 1992). Finally, those individuals could move to the surface at night to feed on high quality food such as diatoms. While chlorophyll *a* concentrations were high throughout the water column, preferable food such as diatoms might still be more abundant in the surface.

Pseudevadne tergestina contained significant higher gut pigment content during the day than during the night, suggesting that the animals were feeding more actively during the day. Diel feeding rhythm existed in *P. tergestina* in the absence of DVM. Such observation further suggests that *P. tergestina* is a predator (Bainbridge

1958; Bryan 1972; Schram 1986) which requires light to feed visually on small flagellates and other microplankters.

3.6 Conclusion

Different species of marine cladoceran showed different patterns of spatial and temporal distribution. Reverse DVM was exhibited by *Pleopis schmackeri*. *Podon* sp. showed daytime inshore aggregation but migrated to offshore regions at night. *Penilia avirostris* females with large embryos performed significant normal DVM. Within the same species, the more conspicuous individuals avoided the surface water and stayed in the bottom during the day. The data presented here are consistent with the hypothesis that the vertical migration exhibited by marine cladocerans was ultimately related to avoid visual predation.

Maturation of embryos in marine cladocerans appeared to be triggered by darkness. In both *Pseudevadne tergestina* and *Penilia avirostris*, the proportion of females with more mature embryos were higher during the night than during the day. *P. tergestina* exhibited pronounced reproductive periodicity by maturation of brood only at night.

The feeding activity of *Penilia avirostris* and *Pseudevadne tergestina* was probably not related to DVM because feeding rhythms existed in the two populations in the absence of DVM. Light seemed to play an important role in controlling the diel feeding rhythm of the two marine cladocerans. Light decreased the feeding activity of *P. avirostris*, but the feeding activity of *P. tergestina* was enhanced by light during daytime.

Herbivorous *Penilia avirostris* fed at night and the females with large embryos (the most conspicuous group) stayed in deeper waters during the day probably to minimize the risk of visual predation. In contrast, *Pseudevadne tergestina*, *Podon* sp. and

Pleopis schmackeri possess large compound eyes and strong raptorial appendages for feeding on microplankters. Their surface- and inshore-dwelling behaviours, as well as the high feeding intensity of *P. tergestina* during the day suggest that light was essential to the feeding activities. Like *P. avirostris*, podonids are also vulnerable to predation by fish. Since feeding increased the visibility of podonids to visual predators, podonids have also developed mechanisms to reduce the risk of visual predation. Larger individuals tended to remain in deeper waters during daytime. *P. tergestina* developed extremely transparent carapace to reduce the conspicuousness and carried pigmented-eyed embryos only at night.

Data on the distribution and abundance of potential predators of marine cladocerans should be collected to provide better estimate of the actual impact of predation. Moreover, development of good culture techniques on marine cladocerans is essential to begin experimental studies on important biological problems such as the effects of temperature, salinity and food on growth and reproduction (Egloff *et al.* 1997). Mechanisms controlling the distribution, migration and feeding behaviour of zooplankton are likely to be species specific, or even habitat specific. However, there is no doubt that a more complete understanding of the ecology of marine cladocerans will, in the long term, help plankton biologists in their effort to construct a more accurate view of the world of the plankton.

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